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EFFECTS OF OVIPOSITION SUBSTRATE ON LIFETIME FECUNDITY OF THE TERRESTRIAL PULMONATE *BRADYBAENA SIMILARIS*

T. ASAMI[1] AND K. OHBAYASHI[2]

Abstract   We tested whether the type of substrate or the size of container affects egg production of the land snail Bradybaena similaris *Férussac. The purposes were to test if the standardized conditions affect the temporal pattern of lifetime fecundity and if convenience can be achieved without significant loss of fecundity in experimental conditions. Adult pairs began to oviposit earlier in humus than in sand. In the small containers, oviposition was more frequent in sand than in humus, once oviposition began. However, the total number of eggs produced did not differ significantly between the different substrates or sizes of container. The sand and small flowerpot used in the current methods are relatively efficient laboratory conditions for oviposition of* B. similaris.

Key words   Model species, Oviposition, Breeding technique, Clutch size, Gastropoda, Bradybaena, Fecundity.

INTRODUCTION

Bradybaena similaris Férussac probably originated in Southeast Asia but has been spread widely around the world. In Japan it occurs abundantly in suburban areas on most islands, especially where invasive grasses and shrubs are dominant. *B. similaris* has many advantages as an experimental model for studies of the genetics, ecology, and evolution of pulmonates: 1) it exhibits shell colour and banding polymorphisms; 2) the genetics of these polymorphisms have been clarified by experimental crosses (Komai & Emura, 1955); 3) the snails are small (12 mm shell diameter); 4) generation time is short (three months in the laboratory; Emura, 1932) compared with one to three years in the species listed above; 5) laboratory breeding is easy; 6) behaviour is easily observed (Asami, Cowie & Ohbayashi, 1989); and 7) dense populations in small areas are common, allowing easy collection of large samples from single populations. To take full advantage of *B. similaris* as a model animal, the simplest and most efficient laboratory breeding conditions must be developed. However, few studies have documented even basic traits of life history of this species under manipulated environments since Emura (1932).

For empirical laboratory studies using living organisms, it is important to determine the most appropriate and efficient breeding conditions based on exact knowledge of life histories. Molluscs in general are difficult to raise and breed in captivity. However, some pulmonates are relatively easy to breed, and for example, ascertaining the genetic basis of the shell colour polymorphism by experimental crosses in snails such as *Cepaea* has played a key role in advancing our understanding of the ecological genetics of visible variation (Murray, 1975; Jones, Leith & Rawlings, 1977; Clarke, Arthur, Horsley & Parkin, 1978; Cain, 1983).

Basic laboratory regimes for breeding land snails have been described for a variety of species: for example, *Cepaea nemoralis* (Hunter & Stone, 1986), *C. hortensis* (Murray, 1963), *Helix aspersa* (Cowie & Cain, 1983; Lazaridou-Dimitriadou, Alpoyanni, Baka, Brouziotis, Kifonidis, Mihaloudi, Sioula & Vellis, 1998), *Theba pisana* (Cowie, 1984a), *Achatina fulica* (Pawson & Chase, 1984), *Archachatina marginata* (Nisbet, 1974), *Bradybaena pellucida* (Asami, Fukuda & Tomiyama, 1993), *Partula suturalis* and *P. taeniata* (Murray & Clarke,

[1] Department of Biology, Shinshu University, Matsumoto-shi, 390-8621, Japan.
E-mail: asami99@gipac.shinshu-u.ac.jp.
[2] Department of Biology, College of Arts and Sciences, University of Tokyo, Komaba, Meguro-ku, Tokyo 153-0041, Japan. E-mail: kakoh@dolphin.c.u-tokyo.ac.jp

1966), *Ashmunella proxima* and *A. lenticula* (Babrakzai & Miller, 1984), *Mesodon normalis* (Stiven, 1995) and *Triodopsis albolabris* (McCracken & Brussard, 1980). However, the various regimes adopted differ and results are thus not strictly comparable between different studies. Moreover, simplification of laboratory conditions that maximize lifetime reproduction and permit efficient experimental replication and maintenance over multiple generations have seldom been explicitly explored or presented with critical comparisons. Instead, empirical knowledge and techniques for breeding tend to be traditionally maintained. Thus in the absence of simple methods established in the literature research with land snails often begins with trial and error in attempts to breed locally available species.

In this study, we examined the effects of substrate type and container size on the lifetime fecundity of *B. similaris*. The purposes were 1) to determine the best regime for easy experimental manipulation and replication without significant reduction of fecundity, as the basis for further applications, and 2) to investigate patterns of lifetime oviposition in standardized conditions.

Materials and Methods

We employed a balanced two-factorial design (2 substrate types x 2 container sizes) with four replicates. Each replicate consisted of one pair of adults in a single container, giving a total of 16 pairs. The substrates were humus from a deciduous forest and sand from a riverside, purchased from a horticultural store. The containers were unglazed clay flowerpots, either large (upper diameter: 25 cm; height: 11 cm) or small (upper diameter: 12 cm; height: 10 cm).

The flowerpots were filled with substrate, leaving an open space of 3 cm to the upper edge of the pot. The pots were then sterilized at 120°C for two hours. To maintain constant high humidity (over 90%) in the open space inside the pots, we kept the bottom of each pot in water 1 cm deep, and the top covered by a transparent acrylic plastic sheet.

We collected fifty juvenile *B. similaris* from a 200 m² area in Akishima, Tokyo, and raised each individual separately in a polystyrene box (11 x 8 x 3 cm), the bottom of which was lined with moist paper towel. Food was oatmeal, chicken egg shell with the shell membrane and dry cat food, ground and mixed in the proportions 5:3:1 by volume. After the shell lips were complete, indicating maturity, four pairs were randomly assigned to each treatment, with each pair maintained in a separate flowerpot. Especially large or small adults were not used, because, given the small number of replicates, we wished to avoid any possible size related bias.

About 1 g of the above food, which was more than a pair of snails could finish in several days, was placed on a round concave glass plate (a 3 cm diameter watch glass) in the center of the flowerpot. Every two or three days we searched the substrate to a depth of 4 cm for eggs with a spoon, renewed the food on the watch glass, replaced the lid, and removed faeces from the inside wall and substrate surface in each pot. We recorded oviposition of each pair until either partner died, to compare fecundity while individuals could continue mating. Although egg production using stored sperm could continue after the death of one partner, we did not include it in the present experiment. The experiment was done at 25°C in a daily regime of 16 hr light and 8 hr dark.

Results

The snails burrowed into the substrate to lay their eggs. Otherwise, they seldom buried

TABLE 1

The oviposition patterns observed through the life span of paired *Bradybaena similaris*

| Substrate	Pot #	Small container # Days to first ovip.	# Days survival	# clutches	Total # eggs	Pot #	Large container # Days to first ovip.	# Days survival	# clutches	Total # eggs
Humus	1	21	174	48	411	1	19	361	81	685
	2	26	532	132	1014	2	4	125	37	397
	3	28	357	71	698	3	18	171	34	226
	4	36	268	44	503	4	44	304	55	578
	Mean	28	333	74	657	Mean	21	240	52	472
Sand	1	41	168	31	316	1	44	206	34	250
	2	28	350	65	879	2	90	389	58	892
	3	28	364	85	1065	3	85	251	30	459
	4	88	270	35	425	4	44	246	37	416
	Mean	46	288	54	671	Mean	66	273	40	504
Grand mean		37	311	64	664		44	257	46	488
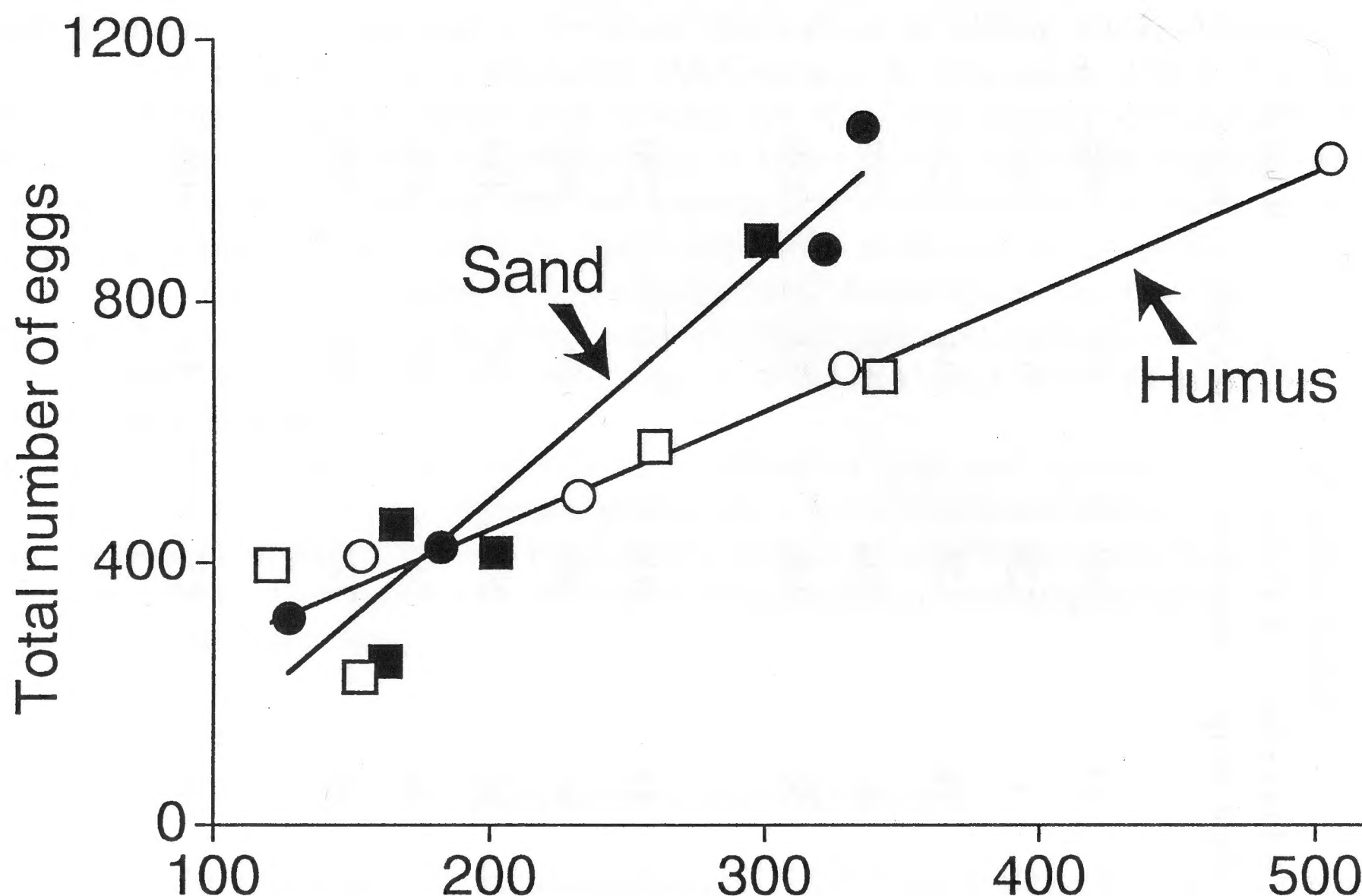
Fig. 1 Regression of the total fecundity on the survival period (days) ○ Small container with humus. □ Large container with humus ● Small container with sand ■ Large container with sand. Regression equations for the humus and the sand are in Table 2, obtained by pooling large and small containers.

themselves. Analysis of faecal contents showed that they ingested little of the substrate. Thus, substrate type was unlikely to have influenced behaviour or to have provided different nutrient resources.

Pairs kept on humus began oviposition earlier than those on sand (two-way Kruskal-Wallis test: H = 7.0; P < 0.01), but there was no significant difference between the large and small containers (H = 0.18; P > 0.50; Table 1). There was no difference in survival (number of days to either partner's death) between substrate types (Breslow test: P = 0.84) or container sizes (P = 0.42). Neither substrate nor container size affected the total numbers of eggs (ANOVA, F = 0.03, and 1.57, respectively; P > 0.20 in both cases) or clutches produced (two-way Kruskal-Wallis test, H = 1.59; P > 0.10 in both cases).

We tested dependence of the total number of eggs on the survival period after the first oviposition by linear regression (Table 2). In spite of a limited replication size (four), the coefficients of determination (r^2) were relatively high, indicating strong dependency of the lifetime fecundity on survival. The regression coefficients were significant in both the humus and sand treatments in the small containers, but not in the large containers.

TABLE 2
Regression of the total number of eggs to the survival period (days)

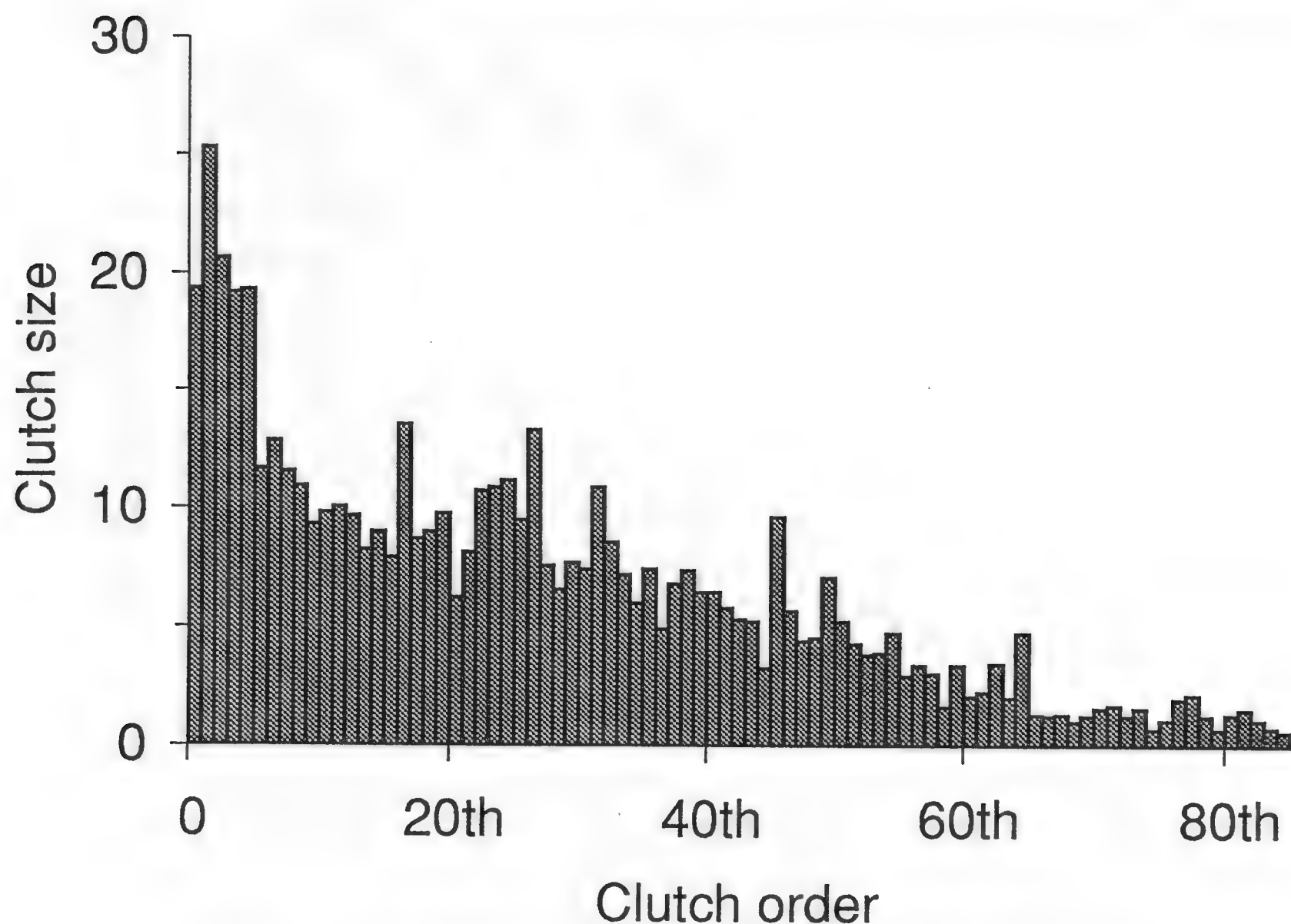| Substrate	Container	Slope	Intercept	r^2	F	Prob.
	Large	1.76	86	.78	6.92	.119
Humus	Small	1.75	123	.99	380.20	.003
	Pooled	1.80	92	.92	73.09	.000
	Large	4.05	-335	.89	16.26	.056
Sand	Small	3.41	-153	.97	58.71	.017
	Pooled	3.65	-232	.93	83.69	.000

Fig. 2   The pattern of clutch-size reduction throughout life.

The slope was significantly larger in the sand than in the humus in the small containers ($t = 4.18$; d.f. = 4; $P < 0.02$). However, between the large and small containers, the slopes did not differ significantly either in the humus ($t = 0.03$; d.f.= 4; $P > 0.5$) or in the sand ($t = 0.63$; d.f. = 4; $P > 0.5$). We therefore pooled the data from the different container sizes and compared the oviposition patterns in the two substrates. In both the substrates, the regression coefficients were significant and differed from each other ($t = 4.25$; d.f.= 12; $P < 0.002$; Fig. 1). These results suggest that pairs of *B. similaris* kept on the sand produced about twice as many eggs per day as those on the humus during their survival period.

The maximum number of clutches produced by any pair was 30. We ranked and compared the sizes of the first 30 clutches produced across the entire experiment using the method of multivariate analysis of variance with repeated measures. No significant differences were found between media ($P = 0.31$) or container sizes ($P = 0.71$). Therefore, we pooled the data from all four treatments to test for any trend in clutch-size over the oviposition period.

We calculated the mean size across the parental pairs for each of the first 85 clutches, in which clutch replicates from at least two pairs were available at every order of clutch production. Because of significant departure from a normal distribution and possible interdependence of clutch sizes within pairs, we employed the runs up and down test (Sokal & Rohlf, 1995). The result indicated that there was a significant reduction in clutch size over time ($t_s = -2.01$; $P < 0.05$; Fig. 2) .

DISCUSSION

Few studies have documented the lifetime fecundity of terrestrial pulmonates under standardized laboratory conditions. In this study, pairs of *B. similaris* were allowed to mate and produce eggs freely under controlled temperature, humidity, light, food, space and substrate to oviposit. The results thus provide a practical basis for experimental breeding of *B. similaris* and for further improvement of breeding efficiency.

On average, a pair of *B. similaris* kept on sand produced 3.4 eggs per day over the survival period of 287 days, while a pair on the humus laid 1.8 eggs per day over 284 days. While both snails remained alive in each pair, mean clutch size declined even though the physical conditions remained nearly constant and food was abundant, as similarly observed in *Theba pisana* by Cowie (1984b). This gradual reduction of fecundity throughout the survival period cannot be ascribed to seasonal environmental changes but likely resulted from ageing, disease or accumulation of parasites.

In its natural habitat, eggs of *B. similaris* are often found in moist litter. The humus we used largely consisted of small pieces of decomposing leaves and twigs, very similar to the composition of natural litter. This resemblance may be the reason that oviposition began earlier in the humus than in the sand. In experimental studies that require easy production of juveniles of closely similar ages, it is desirable to minimize the period before initial oviposition. In this study, on average the snails began to oviposit 24.6 days after being placed in the flowerpots, having been individually isolated prior to this. We have subsequently found that it is best to keep virgin adult pairs well fed and active in clean conditions in the plastic containers as described above for about one week after they attain maturity, rather than transferring them to the plant pots immediately after they attain maturity. They then usually begin to oviposit within one or two weeks.

Despite the significant delay in initial oviposition in the sand, the total number of eggs produced did not differ significantly between the substrates. This means that after the first oviposition, more eggs were produced in the sand than in the humus. This fecundity difference was confirmed by the regression analysis of the output in the small containers. The cause of the difference is not clear. During the experiment, which lasted more than a year, the physical condition of the humus changed because of continuing decomposition in spite of the initial heat-sterilization. In addition, small dipterans began to breed in the humus repeatedly, although we then resterilized all pots (both humus and sand) several times over the period of the experiment. These factors of continuous decomposition and dipteran propagation may have reduced the later fecundity in the humus treatment. It was also a technical benefit of using sand that clutches were more easily found and removed from the substrate than in the pots with humus. Because of these practical advantages of the sand compared with humus, we concluded that sand is by far the most efficient substrate for obtaining the eggs of *B. similaris* in a controlled environment, despite the later onset of oviposition in sand.

Sand was indeed used by Stelfox (1915, 1918) and Oldham (1934) in the earliest experimental crosses of helicids. Soil, however, seems to have been the substrate of common use since then (e.g., Cain & Sheppard, 1957; Cowie & Cain, 1983; Murray & Clarke, 1989). In a preliminary experiment, we tried heat-sterilized black soil as the substrate. We found, however, that the food on the glass plate became overgrown by fungi and bacteria relatively quickly on the soil and that dealing with a particular quantity of dry or moist soil for setting up or maintenance of many replicates requires extra handling time and creation of large amounts of dust. Thus we did not include soil in the present comparison. For easiness of separating eggs from the substrate, Lazaridou-Dimitriadou *et al.* (1998) chose wood chips in preference to soil.

Eggs can also be safely maintained and hatched in appropriate humidity by spreading them on the heat-sterilized sand in a small plastic container, the bottom of which has holes and is kept in water. We keep clutches separately, each in a polyethylene flowerpot (upper diameter: 7 cm; height: 6 cm), with a transparent polystyrene petri dish as a lid. A major advantage of this method is the easy control of humidity and avoidance of the bacterial or fungal overgrowth which often occurs rapidly on a paper substrate, especially after hatching begins. Moreover, it allows ready observation of the hatching success of each egg. Most *B. similaris* hatchlings climb up and stay under the lid. We obtain good hatchability using this method (e.g. 84.5% in *Bradybaena pellucida*; Asami *et al.*, 1993).

The flowerpots we used differ substantially in the substrate area available for oviposition (4.2 times greater in the large pots). The large pot also offers 3.3 times the surface area available for other activities, including all the surfaces of wall, lid, and substrate. Therefore, a density effect on fecundity might have been expected. However, no significant difference was found in patterns of oviposition between the two pot sizes, although this might have been due to the limited size of replication. For oviposition of individuals kept separately after mating (not paired as in our experiment), even smaller flowerpots may suffice.

It is desirable to maintain appropriately high humidity for experimental breeding of terrestrial gastropods in a simple way. We controlled humidity by keeping the pot in a water tray. This method has been employed similarly for breeding helicids (Cain & Sheppard, 1957; Brussard and McCracken, 1974; Murray & Clarke, 1989), a polygyrid (McCracken and Brussard, 1980) and a bradybaenid (Asami *et al.* 1993). Although plastic flowerpots are convenient for maintaining large numbers of clutches because of their light weight and low cost, unglazed clay flowerpots are superior for keeping breeding adults because, in plastic pots, mucus and feces tend to remain wet longer and make the walls dirty faster than in clay pots.

We put the food only on the watch glasses, not directly on the substrate. The use of watch glasses results in increased expense and maintenance time, especially in a large scale of experiment. However, the benefits more than offset the costs: 1) bacterial and fungal growth in the high humidity of the pots is substantially reduced; 2) deterioration of the substrate and container due to the decay of scattered food debris is prevented, thus making it easier to maintain relatively constant conditions; and 3) observation of the relative amount of food consumption in each container is facilitated. Dehydrated powdered food in containers has been similarly used for *Helix aspersa* (Lazaridou-Dimitriadow *et al.* 1998).

For the food, we chose oats, dry cat food, and chicken egg shell with the shell membrane as main sources of carbohydrate, animal protein, and calcium carbonate, respectively. These ingredients also contain a variety of other important nutrients. The shell membrane was included to provide additional proteins and also to make food preparation simpler. Commercially available pet foods, however, should be used with caution because far higher concentrations of pesticide residues are allowed in pet foods than in processed foods for humans. For feeding other land snails, a variety of protein-rich additives have been used such as milk products for several helicids (Albuquerque de Matos, 1984; Cowie & Cain, 1983; Cowie, 1984a), tropical fish food for *C. nemoralis* (Brussard & McCracken, 1974) and *T. albolabris* (McCracken & Brussard, 1980), ground soybeans and baby food for *Acusta despecta* (Kawano, 1976), cat food for *B. pellucida* (Asami *et al.*, 1993), and rodent food for *A. fulica* (Pawson & Chase, 1984). The present proportions of oats, cat food and egg shell can easily be modified for a variety of species. The optimum composition for the growth, fecundity, survivorship and behavioral activities of *B. similaris* needs to be determined by further studies.

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A DEEP-SEA *AMALDA* (GASTROPODA: OLIVIDAE) IN THE NORTH-EASTERN ATLANTIC

Yuri I. Kantor[1] & Philippe Bouchet[2]

Abstract   Amalda sibuetae *n. sp., from off Mauritania in 1733–1855 m, represents the second deepest record for the family Olividae so far. The radular morphology of the new species differs markedly from that in other species currently classified in* Amalda. *No Neogene or Recent Atlantic species appears to be close enough to* A. sibuetae *to be considered its immediate ancestor. The world records of Olividae from depths greater than 400 m are listed.*

Key words   Gastropoda, Olividae, taxonomy, north-eastern Atlantic.

INTRODUCTION

To assess the impact of an environment with weak seasonal variations on deep-sea macrofaunal communities, the EUMELI expedition was carried out in January-February 1991 on board R.V. *Atalante* off Mauritania, focusing on three sites with contrasting trophic conditions (Cosson *et al.* 1997). In a total of 8 box cores taken at the "eutrophic site" in 1590–2040 m, the density of gastropods is only 0.59% of the total benthic invertebrates sampled, whereas aplacophorans and bivalves densities stand at respectively 2.42 and 8.24% of the total. In addition to box cores, sampling was also done by trawling and this yielded two specimens of the olivid genus *Amalda*. These represent not only a new species, described herein, but represent the first finding of Recent species of the subfamily Ancillariinae in the North-Eastern Atlantic.

SYSTEMATIC DESCRIPTION

Olividae Latreille, 1825
Ancillariinae Swainson, 1840
Genus *Amalda* H. & A. Adams, 1853

Type species   Ancillaria tankervillii Swainson, 1825, subsequent designation by Vokes (1939).

Remarks   The subfamily Ancillariinae is generally known in the literature under the name Ancillinae H. & A. Adams, 1853, but the former name has priority. There exists no satisfactory subgeneric classification of the genus *Amalda*, and we have therefore avoided formal use of a subgenus.

Amalda sibuetae n. sp.

Material examined   Holotype (live taken), R/V *Atalante*, off Mauritania, EUMELI 2, stat CP05, 20°30' N, 18°34' W, 1855 m, 06 February 1991; paratype (empty shell), EUMELI 2, stat CP06, 20°31' N, 18°32' W, 1733 m, 07 February 1991. Both in MNHN.

Description (holotype)   Shell oblong-ovate, solid, consisting of one protoconch and

[1] A.N. Severtzov Institute of Problems of Evolution of Russian Academy of Sciences, Leninski prosp. 33, Moscow 117071, Russia.

[2] Muséum national d'Histoire naturelle, 55, rue Buffon, 75005 Paris, France.

Fig. 1 *Amalda sibuetae* sp. nov. **A–E** holotype (**D, E** - coated), **F** paratype, **G–I** radula of the holotype, **G** dorsal view of the radular membrane, **H** enlarged rachidian teeth, **I** part of the rachidian to show the concavity on anterior edge of the tooth. Scale bars = 10 μm (**I**); 20 μm (**G, H**).

probably 4 teleoconch whorls (number of whorls difficult to determine due to extension of primary callus). Protoconch corroded on holotype, bulbous and glossy on paratype (Fig. 2 A–B), protoconch/teleoconch transition indistinct, whorl diameter 800 µm. Spire cyrtoconoid with somewhat mamillate apex, greatest shell width slightly below mid shell height. Last whorl evenly convex on both sides, with relatively narrow base. Primary callus thick and enveloping entire spire, except protoconch, forming impressed false suture, anterior edge delimited by shallow but sharp groove, surface glossy and microshagreened. Secondary callus rather thick, microshagreened, tongue-shaped, covering right ventral side of spire, reaching penultimate whorl and entire parietal region. Aperture lanceolate, roundedly acute adapically, widest medially, occupying 48% of total shell height; siphonal notch moderately deep, symmetrically U-shaped. Outer lip rather thin, slightly opisthocline with low and indistinct blunt basal denticle. Columellar pillar moderately twisted; pleats not pronounced. Anterior fasciolar groove broad and deep, fasciolar band distinct, microshagreened. Posterior fasciolar groove thin, sharp; ancillid groove indistinct, ancillid band weakly differentiated by change in direction of incremental lines. Colour white with slightly yellowish sutural band, overlayed by secondary callus.
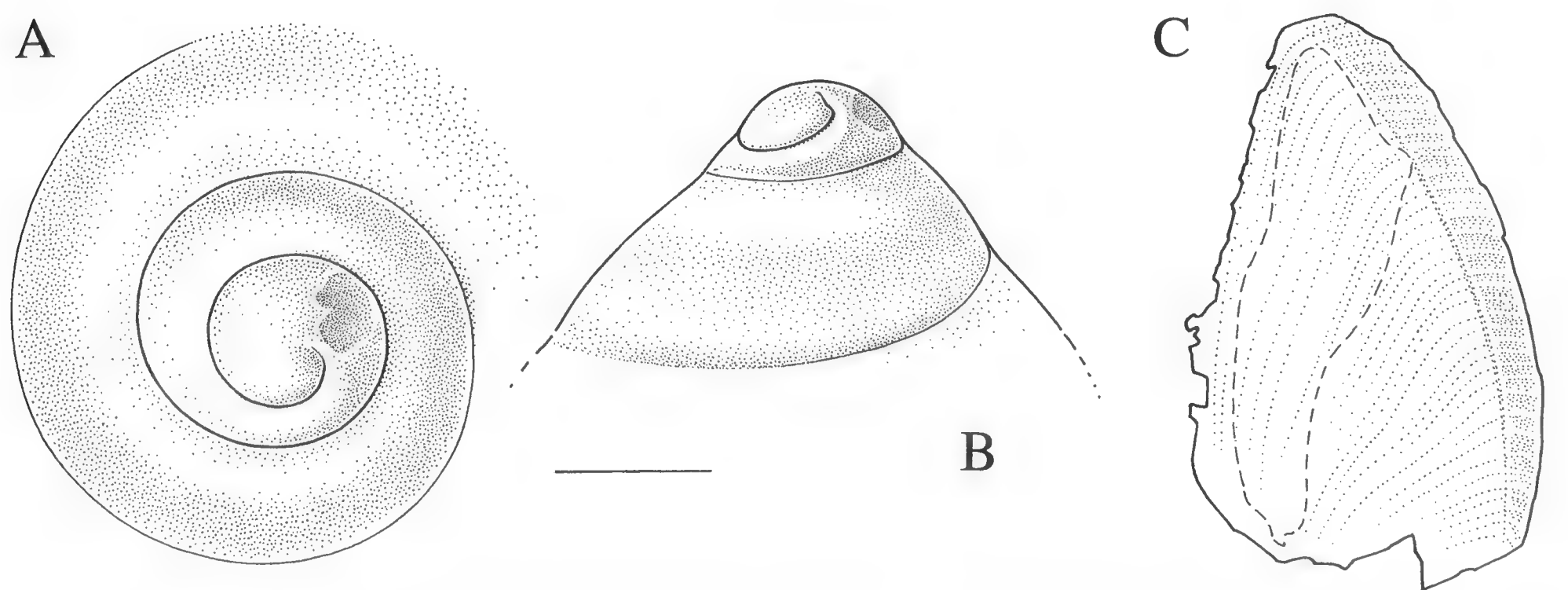
Fig. 2 A, B - protoconch of *Amalda sibuetae* sp. nov., paratype C - operculum, holotype. Scale bars = 1 mm.

Operculum Occupying ⅔ of aperture (but partly worn), very thin and transparent, yellow (Fig. 2C). There is a distinct narrow longitudinal, slightly curved rib on its inner surface. Columellar muscle attachment zone long, ovate.

Measurements Shell height 12.9 mm, diameter 5.4 mm; last whorl height 8.9 mm, aperture height 6.7 mm.

Paratype The paratype (Figure 1F) is a small dead collected specimen, in all respects similar to the holotype. Columellar pillar with 3 weak pleats.

Anatomy Due to the fixation condition we were unable to remove the animal completely from the shell. The specimen appears to be a half mature male with a 1.3 mm long penis (10% of shell height). Although no comparative data are available on penial development in *Amalda*, in mature specimens of other olivids, particularly *Oliva*, penis length reaches 35–40% of shell height [unpublished observations of senior author]. Penis is simple, cylindrical, terminating in small seminal papilla.

Buccal mass terminal, situated close to the mouth opening, contrary to the situation

found in *A. montrouzieri* (Souverbie, 1860) (Kantor, 1991). Radula (Figure 1G–I) rather short, length 600 μm, or 8.9% of aperture height, width 150 μm (2.2% of aperture height) consisting of about 35 rows of teeth only. Shape of rachidians very unusual for Ancillariinae, with very deep notch on the anterior surface and long projection on the posterior, with 3 long and narrow cusps, the central one being the largest. On the midline of the tooth on its anterior edge there is a concavity with eroded surface (Figure 1I). The laterals are of typical shape, unicuspid.

Derivation of Name   The specific name honours Dr Myriam **Sibuet**, of IFREMER, cruise leader of the EUMELI 2 expedition, and a former companion of the second author during many cruises in the North-East Atlantic.

DISCUSSION

The discovery of *Amalda sibuetae* off Mauritania is unexpected, since *Amalda* was thought to have become extinct in the eastern Atlantic and Mediterranean in the late Miocene (Lozouet 1992). The genus exists however in the tropical western Atlantic, where three species occur in shallow water: *Amalda pacei* (Petuch, 1987), from Honduras, in 50 m, *Amalda venezuelana* (Weisbord, 1962) and *Amalda tankervillii* (Swainson, 1825), both from Venezuela in 10–35 m (Petuch, 1987). Comparison of the new Recent species with European fossil representatives of the genus or with the Recent Caribbean ones did not reveal any close similarities, and *A. sibuetae* appears quite isolated morphologically and geographically in the Atlantic fauna. Two scenarios can account for its occurrence. *A. sibuetae* may be derived from a species from the European Oligocene and Miocene shelf faunas, and through its evolution it acquired morphological changes and migrated to lower bathyal depths. Alternatively, *A. sibuetae* may have its origin in the Caribbean stock, and may have migrated across the Atlantic undergoing significant morphological changes. Both hypotheses are equally possible, since we do not know any Atlantic species of *Amalda* which is close enough to *A. sibuetae* to be considered its immediate ancestor. However, so little is known of the Cenozoic faunas of tropical West Africa that a third scenario deriving *A. sibuetae* locally is equally likely.

The radular morphology of the new species is very different from what is known in other species of *Amalda*. Usually in *Amalda* the rachidian has nearly straight or slightly notched anterior edge (see e.g. Kilburn & Bouchet, 1988: Figs 50–58), with the central shorter than the lateral cusps. Conversely, in *A. sibuetae* the rachidian is very deeply notched anteriorly and the central cusp is significantly longer than the lateral. The overall tooth shape is closer to that of *Entomoliva incisa* (Bouchet & Kilburn, 1991: Figs 10–11) than of true *Amalda*. The rachidian tooth shape is also similar to that of *Ancillaria (Turrancilla) lanceolata* Martens, 1904 (Thiele, 1904: pl.9, Fig. 50). In the latter the teeth are also deeply notched anteriorly, although they lack the semi-rounded posterior projection of *Amalda sibuetae*. At the moment the taxonomy of Ancillariinae is based nearly entirely on shell characters and anatomical studies are necessary before we can re-evaluate the status of many nominal genera and subgenera.

The bathymetric occurrence of *Amalda sibuetae* is equally remarkable. At 1855 m, it is the second deepest record of a species of Olividae in the literature, being surpassed only by *Baryspira longispira* (Strebel, 1908) from subantarctic waters (Table 1). (Beside the published records we have seen in MNHN material containing several undescribed species of Ancillariinae, probably belonging to *Gracilancilla* Thiele, 1925, from the Philippines in 200–840 m, Reunion in 410–1180 m, and off Brazil in 450–1555 m). Ancillariines occur mainly on the midshelf, at depths between 30 and 200 m, and only

TABLE 1

Published records of Recent species of Olividae from depths below 400 m

Species	Range	Depth (m)	Source
Amalda aureomarginata Kilburn & Bouchet, 1988	Chesterfield, New Caledonia	300–580	Kilburn & Bouchet (1988)
Amalda bathamae (Dell, 1956)	New Zealand	140–882	Powell (1979), Marshall (pers. com.)
Amalda benthicola (Dell, 1956)*	New Zealand	358–1019	Dell (1956), Marshall (pers. com.)
Amalda fuscolingua Kilburn & Bouchet, 1988	New Caledonia	300–450	Kilburn & Bouchet (1988)
Amalda hilgendorfi (Martens, 1897)	SE Asia, Coral Sea	315–600	Kilburn & Bouchet (1988)
Amalda mucronata (Sowerby, 1830)	New Zealand	15–460	Marshall (pers. com.)
Amalda sibuetae n. sp.	Mauritania	1855	this paper
Ancilla abyssicola Schepman, 1911	Makassar Strait	1301	Schepman (1911)
Ancilla edgariana Schepman, 1911	Ceram Sea	835	Schepman (1911)
Ancilla siberutensis Thiele, 1925	Sumatra	750	Thiele (1925)
Ancilla sumatrana Thiele, 1925	Sumatra	470–660	Thiele (1925)
Ancilla ventricosa Lamarck, 1822**	Tanzania	404–463	Martens (1904)
Ancillaria lanceolata Martens, 1904	Tanzania	404–463	Martens (1904)
Baryspira longispira (Strebel, 1908)	SW Atlantic	2677	Strebel(1908)
Entomoliva incisa Bouchet & Kilburn, 1991	New Caledonia	400–700	Bouchet & Kilburn (1991)
Olivella apicalis Kay, 1979***	Hawaii	500 700	Kay (1979)

* Originally described as a subspecies of *Baryspira novaezelandiae* (Sowerby, 1859), but treated as a distinct species by Marshall (1996). ** Record considered unconfirmed or doubtful by Kilburn (1981). *** Although described in *Olivella*, which constitutes a separate family Olivellidae, it probably belongs to *Gracilancilla*.

14 species have been recorded from depths below 400 m, all of them in the tropical Indo-Pacific or New Zealand. A small radiation has apparently taken place in New Caledonia with two genera and four species, and in Indonesia with two genera and five species in the 300–600 m depth range (Table 1).

ACKNOWLEDGEMENTS

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CORIOCELLA SAFAGAE N. SP. A NEW LAMELLARIID (GASTROPODA: PROSOBRANCHIA) FROM SAFAGA, RED SEA, EGYPT

W. Wellens M.D.[1]

Abstract   The description of C. safagae *is based on three specimens collected alive in the Red Sea near the city of Safaga, Egypt. This species resembles other lamellariid species in having five dorsal bosses* (Chelyonotus tonganus *(Quoy & Gaimard, 1825);* Chelyonotus semperi *(Bergh, 1886) and* Coriocella hibyae *Wellens, 1991) but differs by the body form, the aspect and position of the dorsal bosses, the colour and the radula.*

Key words   Lamellariidae, Coriocella, Chelyonotus, *Red Sea, Egypt.*

INTRODUCTION

Lamellariid species-of the genus *Coriocella* de Blainville (syn.: *Chelyonotus)* are characterised by a massive body ranging from 2 to 8 cm in length when measured alive, and having 2 to 6 dorsal bosses. The small shell with a large last whorl is very thin and internal. The species are widely distributed throughout the Indo-Pacific. They are found from the intertidal zone to depths of 30 m.

This new species is considered very rare because only 3 specimens were found throughout 16 annual shell collecting trips, each of a fortnights duration. These expeditions involved 4 participants searching on the fringing reefs and 2 scuba divers exploring deeper waters.

MATERIAL EXAMINED

Holotype   Specimen #1 (Table 1) was found on the coast of the Red Sea (May 1992) in subtidal water (-2 m) on a sandy bottom near coral formations, two km north of Safaga Egypt.

Paratypes   Specimens #2 and #3 were collected (May 1993) in shallow water (30 cm) from the fringing reef at Sharm el Naga, between Safaga and Hurghada, Egypt. All three specimens were captured alive during the day. They were preserved in 5% formaldehyde and after three weeks transferred to 70% ethanol. The internal shell was studied by X-Ray photographs. All measurements were made with callipers. The three specimens are deposited in the Royal Belgian Institute of Naturel Sciences (R.B.I.N.S) I.G N 27.863.

TABLE 1

Measurements of three specimens of C. *safagae* expressed in mm, and indication of sex.

N°	Sex	Animal			Foot		Shell
		length	breadth	height	length	breadth	max. diam.
1	M	31	16	14	11	5	12.5
2	F	26	24	14	9	4	10
3	F	22	14	8	13	7	16

[1] Scientific Associate, Royal Belgian Institute of Natural Sciences, Malacology Section, Vautierstraat 29, B-Brussels.

Description   Habitus. After preservation the general body form is spool shaped with the anterior end pointed and the posterior end rounded (Figs 1–5). The body bears five dorsal bosses which are big, prominent and rounded. They are located close together in the middle of the dorsum. Their volume persists after the death of the specimen. The central dorsal boss is the largest. The surface of the dorsum, including the bosses, is yellowish brown in colour. Small areas are delineated by darker greenish brown lines. The underside is uniform light green apart from a limited area corresponding with the

Figs 1 & 2 Drawings of *Coriocella safagae* the living animal lateral and dorsal view.

1

2
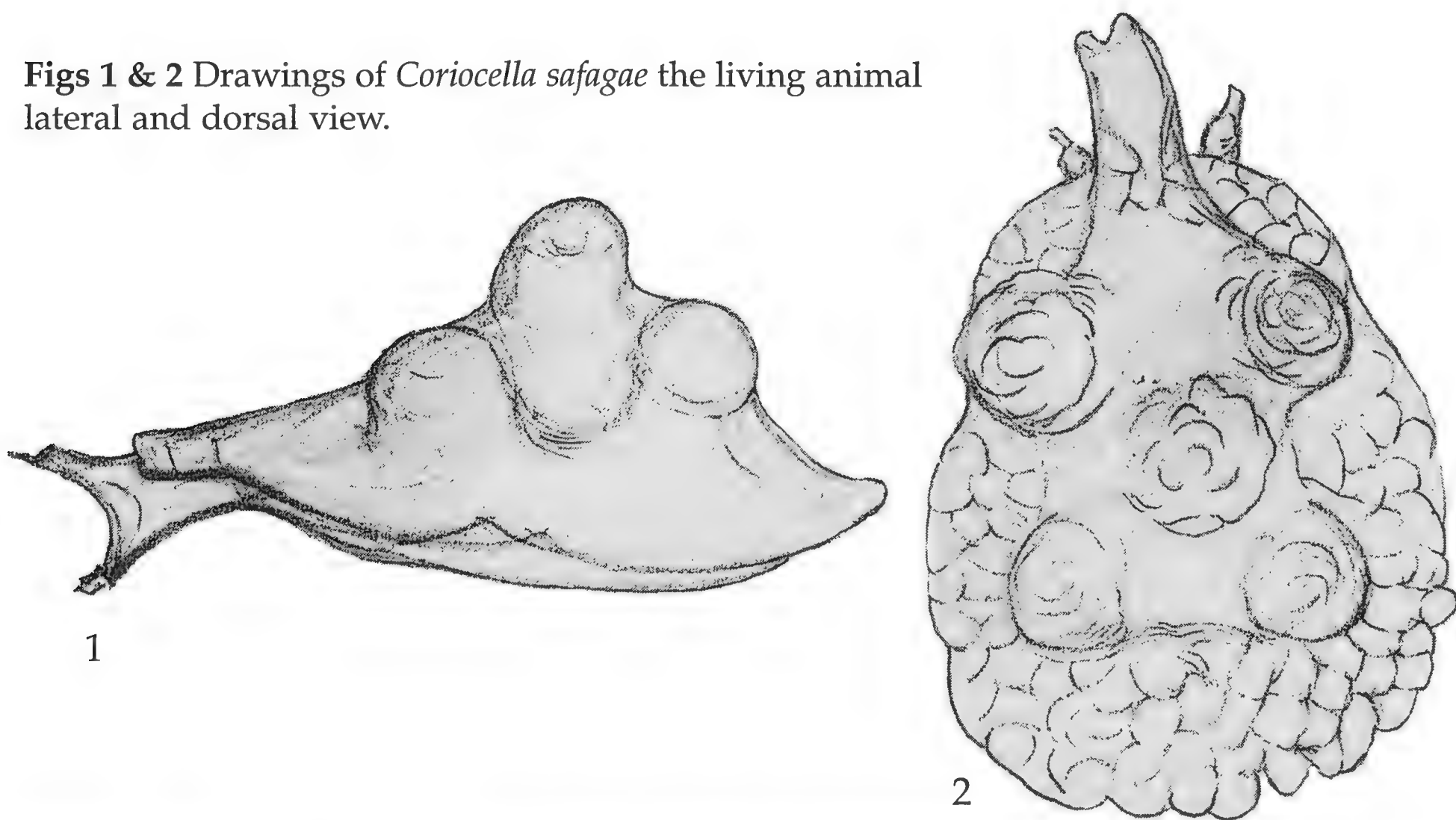
Fig. 3 Photograph of the holotype; left tentacle visible.
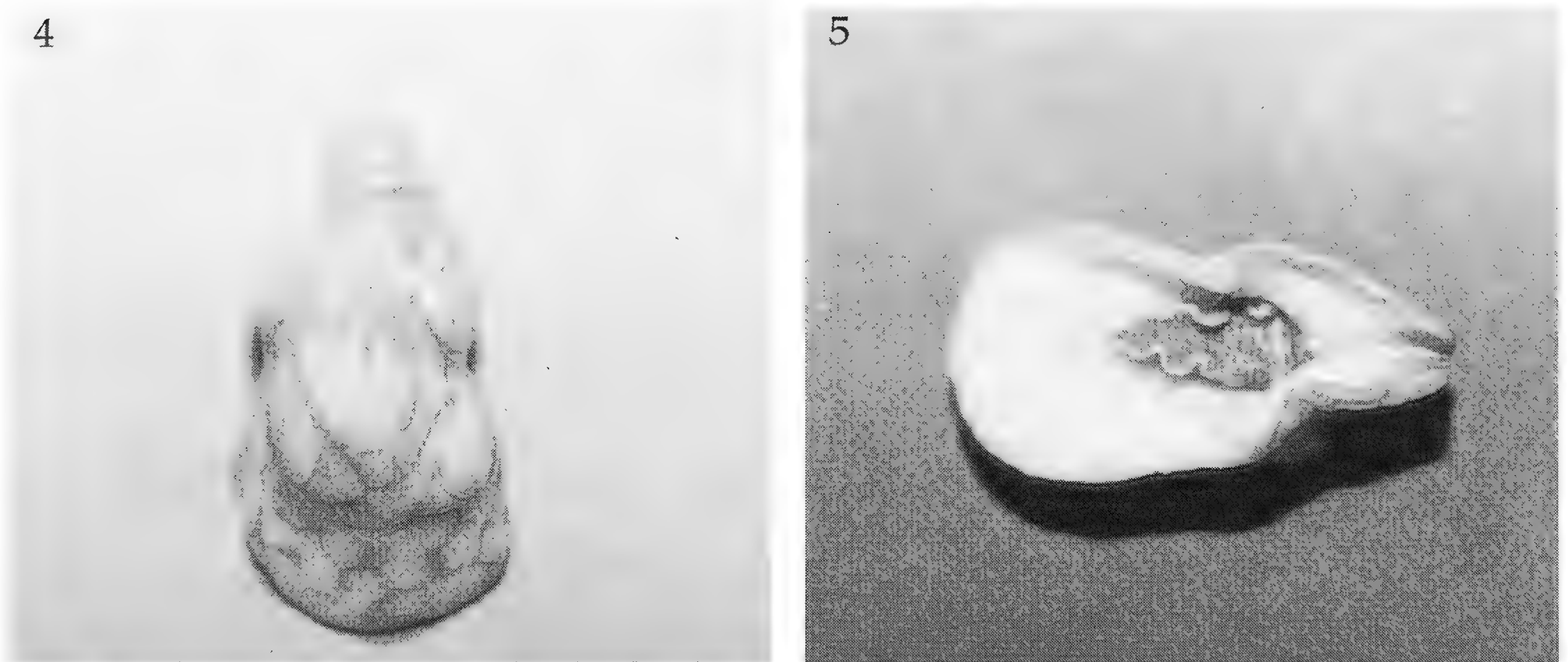
Figs 4 & 5 Photographs of *Coriocella safagae* preserved in 70% ethanol; **4** dorsal view **5** ventral view.

foot which is darker green. The tentacles are about 4 mm long, greyish with yellow tip. The eyes situated at the basal outer side of the tentacles are black in colour.

Anatomy of the holotype. Internal shell. On X-Ray photographs the shells of all three specimens are similar to the shells of the other lamellariid species published (Wellens, 1991;1995). Their maximum diameter is about one half of their body length.

Penis. Length 7.5 mm and a width of 1.9 mm (Figs 6 and 7). It projects from behind the right side of the head. The extreme end of the vas deferens protrudes 0.9 mm beyond the penis tip. At the opposite end the male duct is enclosed in the body wall (characteristic for *Coriocella* spp.).

Jaw. Has a length of 1.4 mm and a width of 1 mm (Fig. 8).
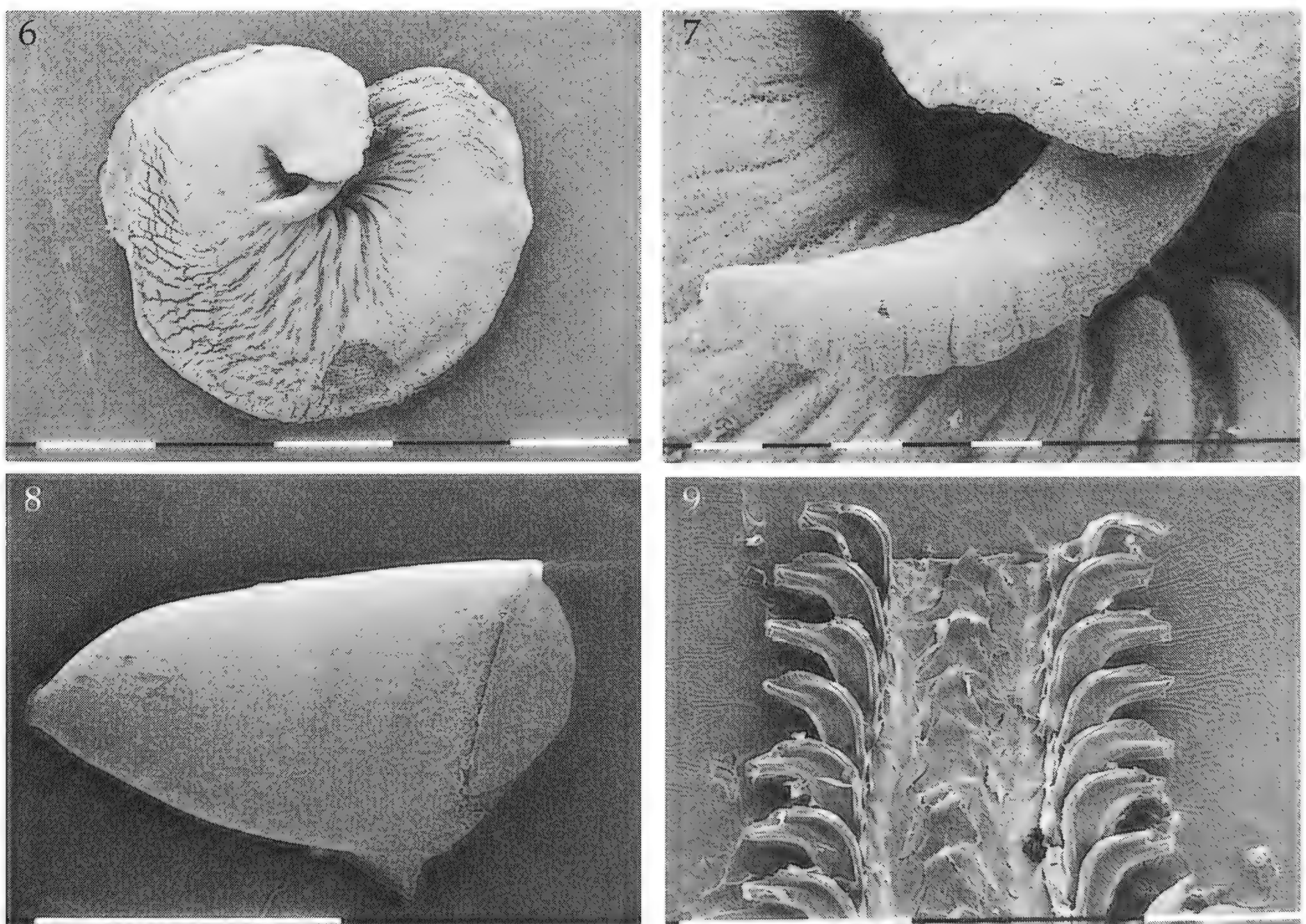
Figs 6 & 7 Scanning Electron Microscope of *Coriocella safagae* **6** Penis Scale bar = 1 mm **7** The vas deferens Scale bar = 100 µm **Fig. 8** The jaw. Scale bar = 1 mm **Fig. 9** Part of the radula. Scale bar = 1 mm.

Radula. Has a total length of 20 mm and a width of 0.9 mm. It is a reduced taenioglossate radula with formula 1–1–1. I studied the middle third where 40 rows of teeth were counted for 1 cm of length. The radula is asymmetrical because the rows are displaced from the longitudinal axis by 40°. (Fig. 9). The rachidian has a length of 270 mm and a base of 200 mm. The left basis is more developed than the right one. The top of the rachidian bears eight denticles on both sides (Figs 10 & 11). The lateral tooth has a length of 710 mm and a maximum width of 220 mm. The external side of the distal cusp (canine protuberance) bears 20 small denticles, the internal side only 7 but larger ones (Figs 12 & 13).

Derivation of name   *Safagae* from **Safaga** the type locality.

DISCUSSION

So far I have studied four Lamellariid species with five dorsal bosses: *Coriocella safagae* from the Red Sea Egypt; *Chelyonotus tonganus* from Tonga in the South Pacific; *Chelyonotus semperi* from the Moluccas, Indonesia; and *Coriocella hibyae* from the Republic of the Maldives (Fig. 15). They are separated by their body form, by aspects of their dorsum, by their colour and by anatomical features. Comparisons of body form and dorsum are illustrated from life drawings in Figure 14 and these are summarised in Table 2.

Comparisons of the radula, of the four species with five bosses, were made on the middle third sections and these are summarised in Table 3. It was only possible to study the radula from a single specimen of each species and therefore the intraspecific variability is not known. Tentatively the radula of *C. safagae* most resembles that of *C. hibyae*
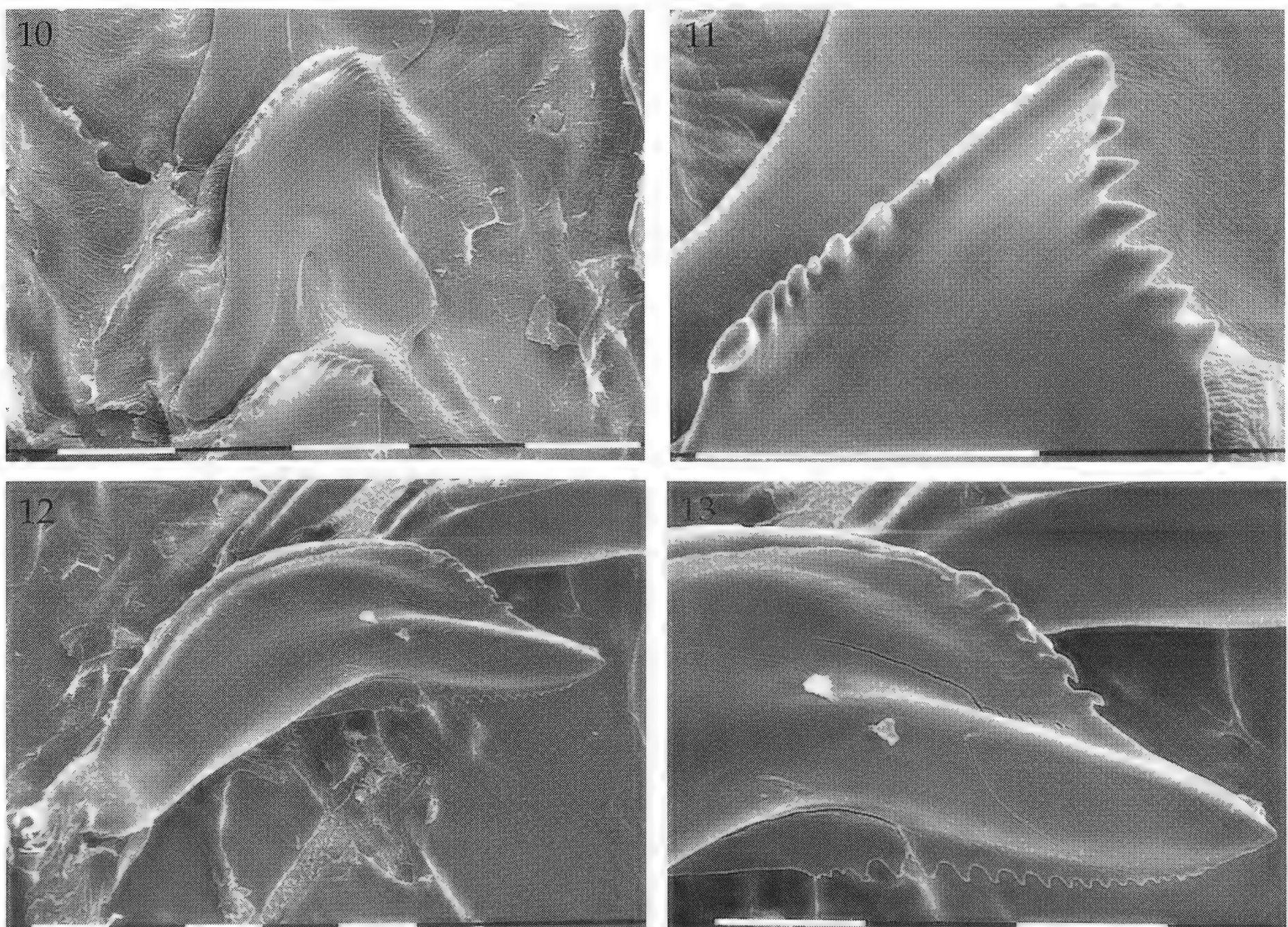

Fig. 10 The rachidian. Fig. 11 The top of the rachidian. Fig. 12 The lateral tooth
Fig. 13 The top of the lateral tooth. All scale bars = 100μm.

TABLE 2
Summary of characters of the four holotypes studied

Specimen	length	body form	bosses	dorsal fields	dorsal colour
C. safagae ♂	31 mm	spool shaped, anterior end pointed, posterior end rounded	rounded, big prominent close together on middle of dorsum; remain after death	yes	yellowish brown
Ch. tonganus ♀	82 mm	ovoid, anterior end rounded, posterior end pointed	rounded, big, not prominent, close together on anterior end; absent after death	yes	black
Ch. semperi ♂	60 mm	spool shaped anterior end pointed, posterior end rounded	elongated, large separated from each other; middle of dorsum on an elevated mantle part; remain after death	yes	black
C. hibyae ♀	35 mm	spool shaped anterior end pointed, posterior end truncated	large, bulbous spread over the entire body length remain after death	no	dark green

in size, rachidian distorsion, number of rows per cm and size of rachidian teeth.
Vayssière (1912) identified as "*Chelyonotus niger* Bergh 1875 (syn: *Lamellaria nigra* Blainville)" a single specimen from the Bay of Tadjourah (Djibouti; Gulf of Aden). His proposed synonymy is incompatible because *Chelyonotus niger* Bergh has five dorsal bosses and *Lamellaria nigra* de Blainville has only three dorsal bosses (Wellens 1998). This poorly known animal is also different from *C. safagae* for the following reasons: other aspect of the dorsum (fig.165 T XX Plate XI); the form of the penis (fig. 166); the symmetrical aspect of the rachidian; the absence of denticles on one side of its top (fig.167), and the black body colouration. Although apparently from close geographical locations, the distance between Safaga and Djibouti is about 1650 km, the sea surface salinities are quite different. Sverdrup measured a salinity of 40 ‰ at Safaga and 36 ‰ at Djibouti

TABLE 3
Comparisons of the radula

length	width	distortion	number teeth rows	rachidian base	rachidian height	lateral teeth length	lateral teeth width
C. safagae 20 mm	0.9 mm	40°	40	204µm 8 denticles both sides	272µm	714µm 20 external denticles	221µm 7 internal
Ch. tonganus 40 mm	1.5 mm	20°	20	400µm 10 denticles both sides	480µm	1000µm 20 external denticles	400µm 10 internal
Ch. semperi 15 mm	0.8 mm	30°	40	257µm 6 denticles both sides	215µm	772µm 20 external denticles	223µm 5 internal
C. hibyae 27 mm	1.2 mm	20°	20/40	450µm 10 denticles both sides	275µm	1000µm 20 external denticles	274µm 6 internal

14

a

C. safagae n.sp.

b

Chel. tonganus.

c

Chel. semperi.

d
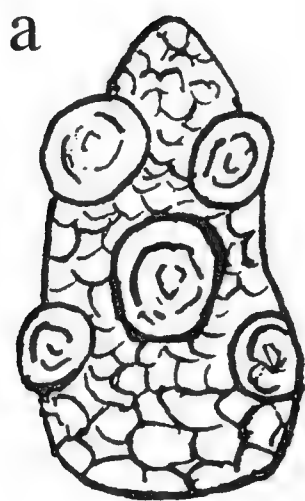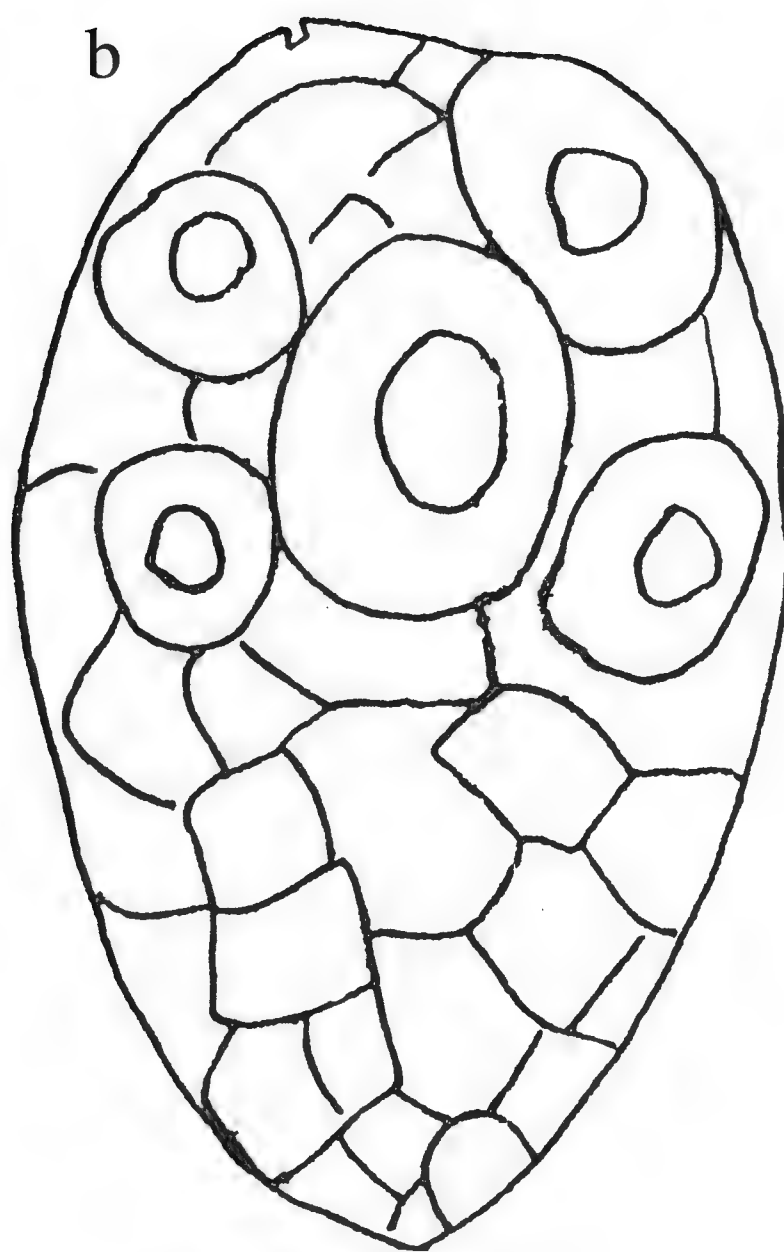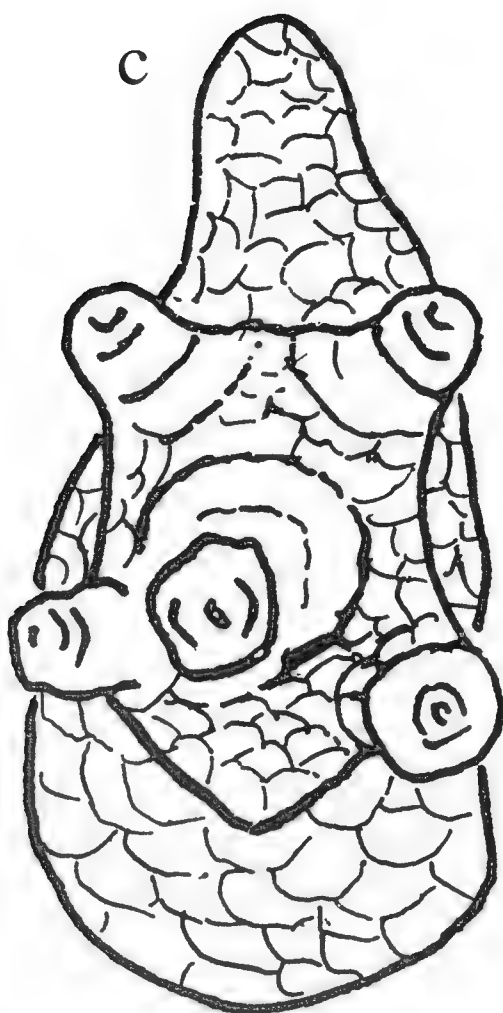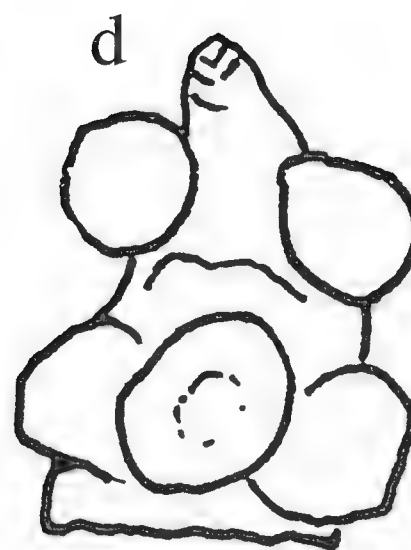
Scale bar
10 mm

C. hibyae.

Fig. 14 Comparative size life drawings of the dorsum of four different species of Lamellariidae with five dorsal bosses.

and from this one can postulate that these related species inhabit rather different environments.

Marcus (1956) wrote " *Lamellaria* is a cosmopolitan genus. The classification of its species must be based exclusively on morphological criteria" and more specifically "Dorsal bosses were considered as specific" (Marcus, 1986/87). Since the number of bosses is generally considered not to vary within a species *C. safagae* is compared with the three other species having five bosses. Although two of them are clearly distinct (Fig.14): *C. tonganus* by the body form, the position of the bosses, the colour as well as radula features and *C. hibyae* by the heavily developed bosses, the general form, the colour and the radula, *C. safagae* does show a certain resemblance to *C. semperi*. However the former species is clearly distinguished by the bosses being arranged on an elevated part of the mantle, size, colour and by its radula.
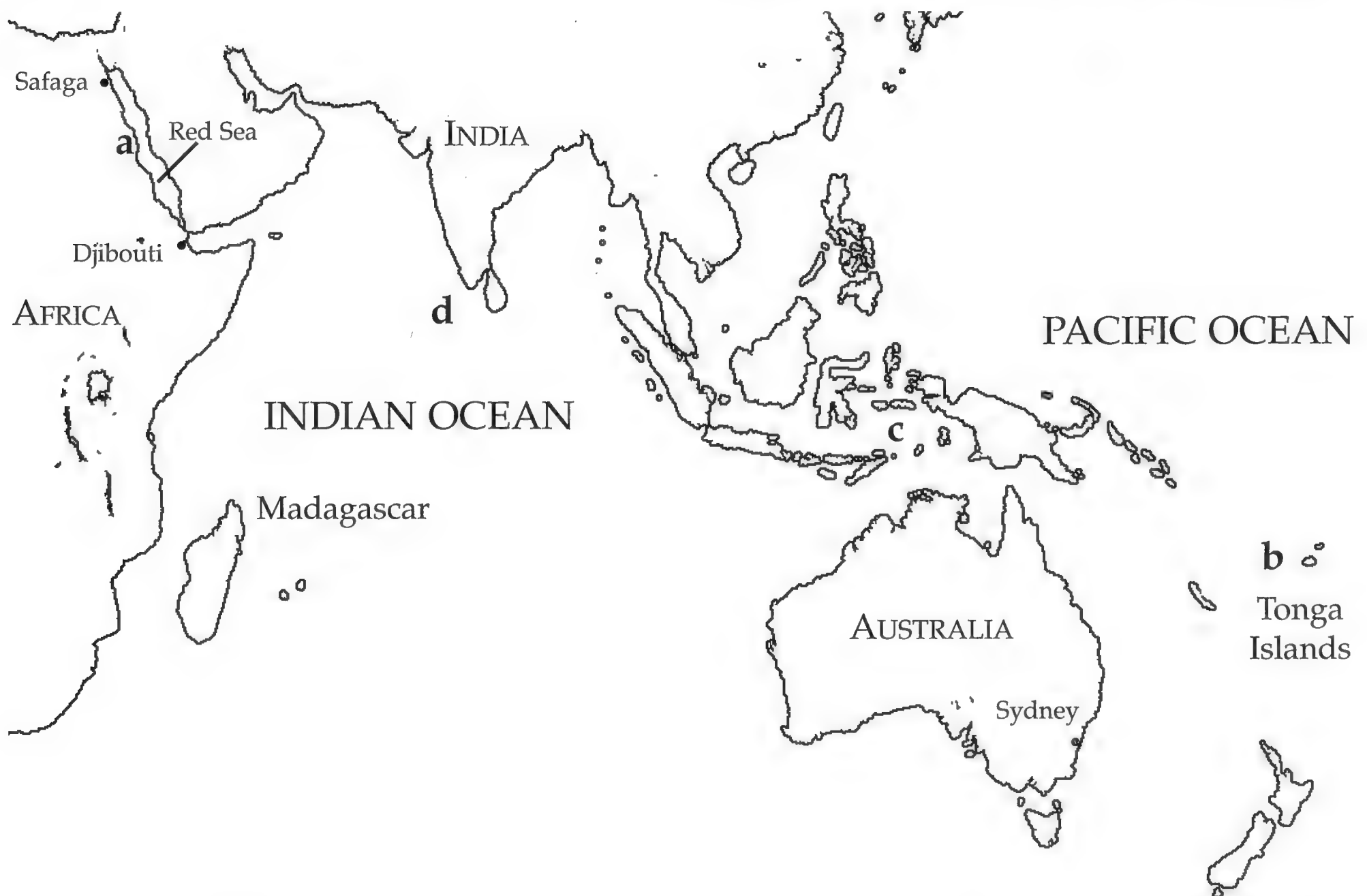
Fig. 15 Geographical map with the location of the 4 lamellarid species with 5 dorsal bosses.
a Red Sea *C. safagae*, **b** Tonga *C. tonganus*, **c** Moluccas *C. semperi*, **d** Maldives *C. hibyae*.

Thiele (1931) wrote that *Coriocella* Blainville, 1824 is a synonym for *Chelyonotus* Bergh, 1835 because in both the male duct is enclosed in the body wall. *Coriocella* is the oldest name and because our new species presents the same anatomical characters the new species is assigned to *Coriocella*.

ACKNOWLEDGEMENTS

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MOLLUSCS IN COPPICE WOODLAND

A.J. MILLAR[1] & S. WAITE[2]

Abstract   A coppice woodland in Sussex has been surveyed for molluscs (quantitatively for snails and qualitatively for slugs) and measurements taken of pH, free chalk, litter and vegetation, with the aim of determining whether coppicing has an effect on snails. The fauna and population structure are described. No direct correlations have been found between age of coppice compartment and either diversity or abundance of snails, although significant relationships were obtained between age and litter depth and between age and percentage vegetation cover. However, two species of snail were found mainly in the earlier or later stages (Vitrina pellucida, Oxychilus alliarius). *A negative relationship exists between snail diversity and abundance, and may reflect, in this particular woodland, the increased dominance of* Carychium tridentatum. *However, comparison with other studies indicates that a positive relationship between diversity and abundance is also possible.*

The pH has a significant, positive relationship with snail species richness and abundance in the community as a whole. A number of individual species (Carychium tridentatum, Discus rotundatus, Aegopinella pura, Vitrea contracta, Pomatias elegans *and* Vitrina pellucida) *show strong positive relationships with pH, and others* (Nesovitrea hammonis *and* Punctum pygmaeum) *show pronounced negative relationships. Litter depth and litter percentage cover appear to play an important role, with several species achieving peak numbers at 2 cm depth of litter. Soil particle size may also be a factor affecting richness and abundance. It is suggested that the main effects of coppicing on snails could be caused by the associated initial reduction in litter. This would affect litter dwelling species most. The arboreal and dead-wood favouring species are likely to be at a relatively low level of abundance because of the removal of dead wood associated with coppicing.*

INTRODUCTION

Coppicing, as a form of management of woodlands, is increasing and many previously neglected coppiced woodlands are now being managed in this way. The regular cycle of disturbance which results from coppicing has been shown to have mixed benefits to the flora and fauna. There is considerable debate about the benefits or otherwise of coppicing (e.g. Booker & Tittensor, 1992; Fuller & Warren, 1991; Kirby, 1992; Patrick & Hendry, 1982; Peterken, 1991; Sterling & Haumbler, 1988; Whitbread & Jenman, 1995) as the practice may be detrimental to species requiring undisturbed microenvironments or dead wood. The effects on the vegetation are well documented and several studies have measured physical parameters in woodlands including coppiced woodlands (e.g. Frankland, Ovington & Macrae, 1963; Ash & Barkham, 1976; Patrick & Hendry, 1982; Barkham, 1992). Some animals have been found to prefer certain stages in the coppice cycle (e.g. Hicks, 1986; Sterling & Hambler, 1988; Welch, 1969). Animals and plants favouring dead wood or stable habitats, such as old-wood lichens and wood-boring beetles, are rare in coppice woodland (e.g. Fuller & Warren, 1995; Kirby, 1992; Sutherland & Hill, 1995).

A few studies have referred to the possible relationships of snails and coppicing. Berry (1973) suggests that coppicing has a devastating effect. Paul (1975) suggests that in Hayley Wood the immediate effects are undesirable but later some species benefit more than others. Subsequently, Paul (1978) felt that most of the species present survive coppicing quite well and some might even benefit. Reynolds (1993) carried out a species comparison of a coppiced and adjacent non-coppiced site and Wardhaugh (1996a) calls for further research. There is a great need for detailed information on the effects of coppicing on snails. It is important to understand the potential effects management has on the fauna before a management decision is made. A number of mollusc studies have

[1] Geniefa, Cuckfield Road, Hurstpierpoint, Hassocks, West Sussex, BN6 9LL, UK.

[2] Biology Division, University of Brighton, Cockcroft Building, Moulsecoomb, Brighton, BN2 4GJ, UK.

included measurements of aspects of the environment such as pH, nutrient levels, vegetation cover, in conjunction with the diversity and abundance of molluscs (e.g. Bishop, 1976, 1977a; Cameron ,1973; Hermida, Ondina & Outeiro, 1995a, 1995b; Outeiro, Aguera & Parejo, 1993; Tattersfield, 1990; Valovirta, 1968; Waldén, 1981; Wareborn, 1970, 1992). The aims of the present research were to look at the effects of coppicing on snails.

SITE DESCRIPTION

LOCATION

West Dean Woods Nature Reserve, (SU845155) is a 16.6 hectare, semi-natural, ancient woodland (listed in the English Nature Inventory), leased and managed by the Sussex Wildlife Trust since 1975 from the owners The Edward James Foundation. The site is in West Sussex, approximately 8 km north of Chichester. It is an SSSI and comes within the South Downs Area of Outstanding Natural Beauty.

DESCRIPTION

The woodland, on a gentle south facing slope of the South Downs, has not been cleared recently, although much of the surrounding woodland has been felled and planted with conifers, or cleared for agriculture. However, lynchets have been found in the reserve and nearby indicating that the area was probably cleared for agriculture in Roman or Iron Age times. Records dating back to the early 17th century indicate it has been continuously wooded since then and probably for some considerable time before. A lease of the area dated 1604 mentions "Brigdene Coppice" and there exist coppice stools of between 300 and 400 years old (personal communication, Sussex Wildlife Trust). Although no other documents have survived, the woodland structure and plant species list strongly suggest a history of coppicing. After World War II, coppicing was neglected and in 1976 it was recommenced on an 11 year cycle initially (later changing to a 15 year cycle). The site has been divided into 24 compartments for ease of management, each compartment being accessible on at least one side by a ride or path wide enough for a tractor to pass. Twenty two compartments are of similar area (approximately 0.5 ha) and are actively coppiced. The remaining two are about four times the size of the others. One is an overgrown coppice now tending towards high forest structure and is managed for lichens, the other a grassy open area with a few large oak trees and little understorey vegetation, maintained for its colony of wild daffodils. (Figure 1).

The woodland is predominantly hazel coppice with oak standards and a rich ground flora including bluebells, National Vegetation Classification W10 (Rodwell, 1991). A discussion of vegetation type and its relationship with the snails will be published elsewhere. The reserve lies at an altitude of between 110 m and 160 m above sea level. There are no streams or other surface water on the reserve.

GEOLOGY AND SOILS

The site lies on the Chalk of the Upper Cretaceous overlain by Head deposits, which are thicker at the higher, more gently inclined, northern part of the reserve. The soil varies in depth of between 250 mm and 300 mm, being deeper in the northern part of the site and shallower on the southern part which slopes gently towards the south. The soils are very variable and generally are not calcareous, with pH less than 7.0. Their great variability throughout the wood is believed to be due to the parent Head material being composed of varying proportions of the following: solifluction material derived from the chalk (here mostly decalcified); weathered remnants of the once overlying Tertiary deposits and wind-blown loess (Catt & Hodgson, 1976). The soils are mainly Argillic Brown Earths and in places tend towards Brown Calcareous Earths (Avery, 1980).

PUBLIC BRIDLEWAY

123
(40+)

116
(8)

109
(12)

124
(40+)

115

110

122
(2)

114

111
(11)

PRIVATE HOUSE

121
(3)

113
(10)

112
(5)

120
(4)

108

119

107a

N

118

WOODYARD

105

106

SHEEP FIELD
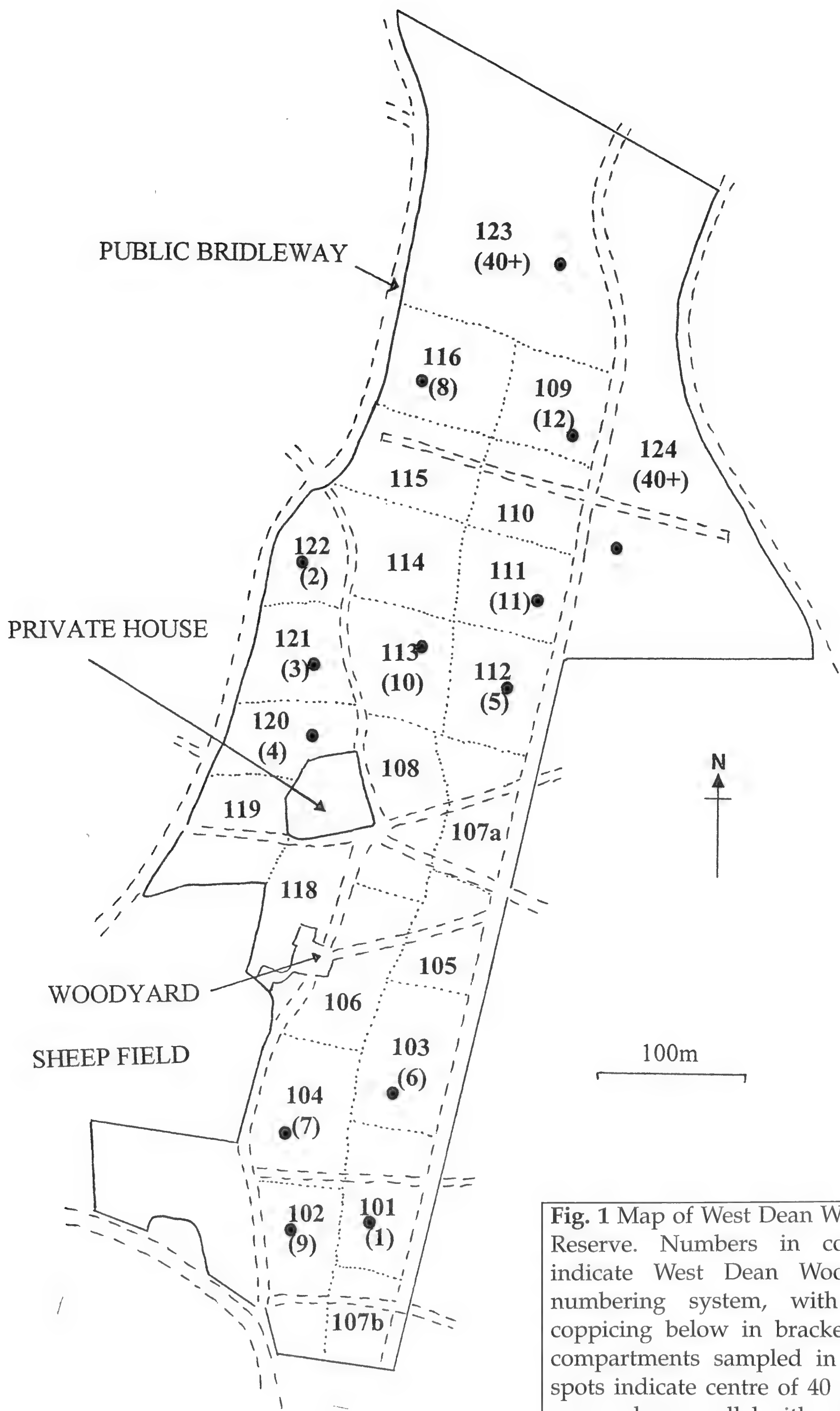
103
(6)

100m

104
(7)

102
(9)

101
(1)

107b

Fig. 1 Map of West Dean Woods Nature Reserve. Numbers in compartments indicate West Dean Woods Reserve numbering system, with age since coppicing below in brackets for those compartments sampled in 1996. Black spots indicate centre of 40 m² sampling areas, edges parallel with and 10 m away from compartment edges.

METHODS

SAMPLING

One compartment of each age from 1 to 12 years, and the two of 40+ years, were chosen for study. (The term 'age' here means the number of years following coppicing, so year 1 means that compartment was coppiced the winter before, i.e. approximately 6 months before). Where there was a choice of two compartments of the same age, the one further from the private house on the reserve was chosen to avoid any introduced or garden species which may be colonising the wood. The anthropophile species *Helix aspersa* and *Monacha cantiana* were found mainly on the paths near the house and woodyard on the reserve but only rarely appeared in the samples. Although the compartments were of approximately similar area (except 40a and 40b), to avoid any differences caused by sampling in different sizes a 40 m² area was selected in each compartment, 10 m from the nearest path or ride to avoid edge effects. Within this 40 m² area four quadrats were chosen using computer generated random coordinates.

This resulted in a total of 56 quadrats each measuring 0.5 m x 0.5 m. Preliminary studies suggested that this was an adequate sample size. Sampling was carried out in as short a time as possible (between 21st May and 19th June 1996) in order to minimise population changes due to breeding, or other seasonal changes. A general mollusc survey was carried out in each of these compartments at the same time, lasting about one hour, and another in October 1996, after rain, specifically for slugs.

At each quadrat before sample collection, measurements were made of the percentage litter cover and average litter depth, moss cover and bare soil. Vegetation cover was estimated for each plant species and because of stratification, cover values of over a hundred percent were sometimes obtained. All litter, twigs, vegetation and loose soil were collected from the quadrat down to a depth where the soil became difficult to remove (approximately 4 cm). This was considered to be the zone in which the snails were living. The samples were oven dried and sieved. Snails were removed by eye from the larger fractions, and under a binocular microscope for the smaller fractions down to 0.5 mm. In this way only the recently hatched juveniles of the smallest snails e.g. *Carychium tridentatum* and *Punctum pygmaeum* are likely to have been missed. Re-examination of some samples leads us to believe that the number of snails which may have been overlooked in the extraction process was less than 10% and would not affect the results significantly. Juvenile *Oxychilus alliarius* were difficult to distinguish from juvenile *O. cellarius,* and so these species were combined and called *O.* sp. Calcareous worm granules, believed to be of the genus *Lumbricus* (Meijer, 1985) were also extracted and counted because in some late-Glacial deposits they have been found to have a close correlation with snail shell numbers (Kerney, 1971; Preece, Kemp & Hutchinson, 1995).

The snails were identified and classified as alive or dead at time of collection, and adult or juvenile. Shells were called adult if they showed characteristic lip modifications achieved on maturity by determinate species such as *Carychium tridentatum, Clausilia bidentata* and *Cochlodina laminata.* Those species which do not modify their lip were considered adult if they possessed more than five-sixths of their potential number of whorls (as given in Kerney & Cameron, 1979). In each category the snails were scored as alive or dead at the time of collection. If the body was seen inside it was scored alive. If roots had penetrated the shell, if the shell was empty or substantially damaged it was scored as dead. In the majority of cases it was quite clear whether the snails had been alive or dead, however, some problems were encountered with *Carychium tridentatum.* The juveniles were sufficiently translucent to determine whether the body was present or not, but many adults were opaque. By careful inspection of the shell at a particular angle the orange coloured part of the body could be seen. All the *Carychium* were double checked and any which were shorter than normal were measured. Only in the case of

one individual did the height to maximum diameter ratio indicate a possible *Carychium minimum* (Watson & Verdcourt, 1952).

pH TESTING

After snail extraction, pH tests were carried out on the sieved fractions from which stones and soil granules larger than 2.5 mm had been removed, in August 1997. The tests were carried out using a 1 : 2.5 ratio of soil (30 g) to distilled water (75 ml) and a standard electronic probe pH meter (model ELE HI9024) into the supernatant liquid (in accordance with section 9.5 of BS1377:Part 3:1990).

CHALK CONTENT

A visual assessment was made of the presence or absence of particles of chalk above 0.5 mm. These were scored as follows: No free chalk - 0, Fewer than 5 pieces - 1, Chalk frequent - 2, Chalk abundant - 3.

ANALYSIS

The diversity of the live snail fauna in each compartment was assessed using the Shannon-Weaver general index of Diversity. This index is largely independent of sample size and provides a robust general index of community diversity (Ludwig & Reynolds, 1988). Relationships between recorded variables were investigated using product-moment correlations analysis (Sokal & Rohlf, 1981). Prior to analysis, all variables were tested for normality using the Shapiro-Wilk test (Minitab, 1996) and, if appropriate, transformed. Snail counts were normalised by a square root transformation, all percentage cover values were arcsine transformed. For each snail species, the relationship between snail abundance and compartment age and pH was assessed by the calculation of a weighted average. This calculation was based on all the quadrats, for species with a total of more than 30 individuals.

$$S_j \frac{\sum_{i=1}^{k} n_{ij} x_i}{N_j}$$

where

S_j = weighted average for pH or age of species j.
n_{ij} = number of individuals of snail species j recorded in plot i.
N_j = total number of snails of species j recorded.
x_i = age or pH value of plot i.

Weighted averages provide a measure of centre of species distribution (niche-centroid) along the environmental gradient measured by the variable x. The weighted standard deviation provides a measure of niche breadth (Ter Braak & Verdonschot, 1995), the values of which are presented in the results section of this paper as percentage coefficients of variations obtained by dividing the weighted standard deviation by the weighted average. Large values imply that the species is widely distributed with regard to either the plot pH or age, low values imply that the species occur predominately within a narrow range of pH or age. The weighted averages values were used to produce a two dimensional species direct ordination (Gauch, 1982). All statistical tests were performed using MINITAB for Windows™ release 11.

Thus, the study allowed us to characterise the snail community present in each coppiced compartment in terms of abundance, community composition and relationship to a limited number of key environmental factors.

Results

General

Details of the means for snail density (m^2), pH and other environmental factors are given in Table 1, and correlation values in Table 2. Ground flora vegetation cover showed relationships with compartment age, in line with what is known about coppice ground flora. Total plant cover positively correlated with age ($p<0.05$). Vegetation cover increased from approximately 80% cover in year one to a peak at 120% in the 5th year and then declined to about 5% by year 12. In contrast depth of litter showed a linear increase from a mean of 1 cm to over 2.5 cm during the first 12 years (Figure 2). The litter depth in the 40+ year old compartments was between 2 and 2.5 cm. There was a significant correlation between compartment age and litter depth ($p<0.01$).

Molluscs

A total of 40 species (including slugs which were not able to be sampled from the quadrats and, therefore, are not included in the analyses) was found alive in the coppiced woodland from both quadrat and survey. Twenty three of these were found in the quadrats alive, with a further two species as dead individuals from the quadrats. Species found are given in Table 3. The densities and constancy (percentage of quadrats in which the live species were found) of the species found in the quadrats are also given in Table 3. *Vallonia excentrica* was represented by a single dead, old shell in compartment 3. A single live specimen of *Candidula intersecta* was found on the wood boundary with the sheep field. Neither of these species, is normally found in woodland.

No Red Data Book species were found at West Dean Woods, however, *Acicula fusca, Limax tenellus, Limax cinereoniger* and *Macrogastra rolphii* are "Notable" species (English Nature Invertebrate Site Register). *Cecilioides acicula, Columella aspera, Pomatias elegans,* and *Oxychilus draparnaudi* are "Local" species (EN Invertebrate Site Register). *A. fusca, L. cinereoniger* and *L. tenellus* are considered to be primary woodland indicator species (Kerney & Stubbs, 1980).

TABLE 1

Data for different aged compartments. Mean of four quadrats and total numbers.

MEANS

Age	1	2	3	4	5	6	7	8	9	10	11	12	40	40
pH	5.6	4.9	5.8	5.7	5.2	5.6	5.5	4.7	5.9	4.7	5	4.8	5.4	4.6
Free chalk	1	0.75	2	1.25	0.5	0.25	1	0.5	1.75	0	0.25	0	1	0.5
Worm granules	55.8	13.3	685	188	6.75	51.5	24	1.25	120	10.8	4.5	0	28.8	0.25
Shell fragments	56.3	53.8	430	155	46.3	64.8	172	12.3	137	22	43.3	26.3	70.3	39.3
Total snails	74.8	30	243	239	170	245	267	72.5	461	38	72.5	104	159	49.5
Live snails	30.5	3	30	74.3	31.3	103	118	42.5	184	14	33.5	57.3	88.5	18.5
Dead snails	44.3	27	213	165	139	143	149	30	277	24	39	47	70.8	31
Litter depth cm	1	1	1.25	2.5	1.5	1.75	1.75	2	2	2.8	3.75	2.5	1.75	2.25
Bare soil %	15	25	1.75	6.75	8.75	10	22.5	27.5	8.75	1.3	0.5	6.25	10	8.25
Litter % cover	2.5	4.25	30	62.5	72.5	41.3	56.3	68.8	43.8	34	89.5	58.8	83.8	69.3
Logs % cover	0	0.5	0	2	0	0	0	0	0	0	0	0	2.5	0
Moss % cover	27.5	17.5	22.5	28.8	5	50	21.3	11.3	48.8	65	10	35.3	6.25	22.5
Veg % cover	80.3	62.5	97.5	116	120	66.3	83.8	49	76.3	76	40.3	4	53.3	79.5

ACTUAL NOS

Live snails total	122	12	120	297	125	410	476	170	737	57	134	229	354	74
Total snails	278	119	973	948	678	980	1067	290	1845	151	290	416	637	198
Species no.(live)	15	8	15	15	12	13	14	13	13	10	12	12	16	14
Total species no.	19	14	22	20	19	18	18	18	18	16	15	15	20	18

TABLE 2

Correlation matrix for the edaphic factors measured. Critical levels: p<=0.10, 0.4973, NSt; p<=0.05, 0.576, *; p<=0.01, 0.708, **; p<=0.001, 0.823, ***. Not significant, NS. WG = Worm Granules.

|	Age	pH	Free chalk	ln(WG+1)	Litter depth	% Litter cover	Total plant cover	No. Snail species	Snail diversity
Age									
pH	-0.468 (NS)								
Free Chalk	-0.506 (NSt)	0.78 (**)							
ln (WG+1)	-0.586 (NSt)	0.881 (***)	0.831 (***)						
Litter depth	0.798 (**)	-0.313 (NS)	-0.432 (NS)	-0.359 (NS)					
% Litter cover	-0.108 (NS)	0.010 (NS)	0.166 (NS)	-0.070 (NS)	0.155 (NS)				
% Plant cover	-0.622 (*)	0.553 (NSt)	0.533 (NSt)	0.673 (*)	-0.379 (NS)	0.049 (NS)			
No. snail species	0.043 (NS)	0.597 (*)	0.347 (NS)	0.347 (NS)	0.142 (NS)	0.158 (NS)	0.275 (NS)		
Snail diversity	-0.003 (NS)	-0.490 (NS)	-0.321 (NS)	-0.376 (NS)	0.061 (NS)	0.597 (*)	-0.008 (NS)	-0.169 (NS)	
Square root total	0.251	0.556	0.39	0.302	0.045	-0.366	0.052	0.535	-0.786
Number of snails	(NS)	(NSt)	(NS)	(NS)	(NS)	(NS)	(NS)	(NS)	(**)
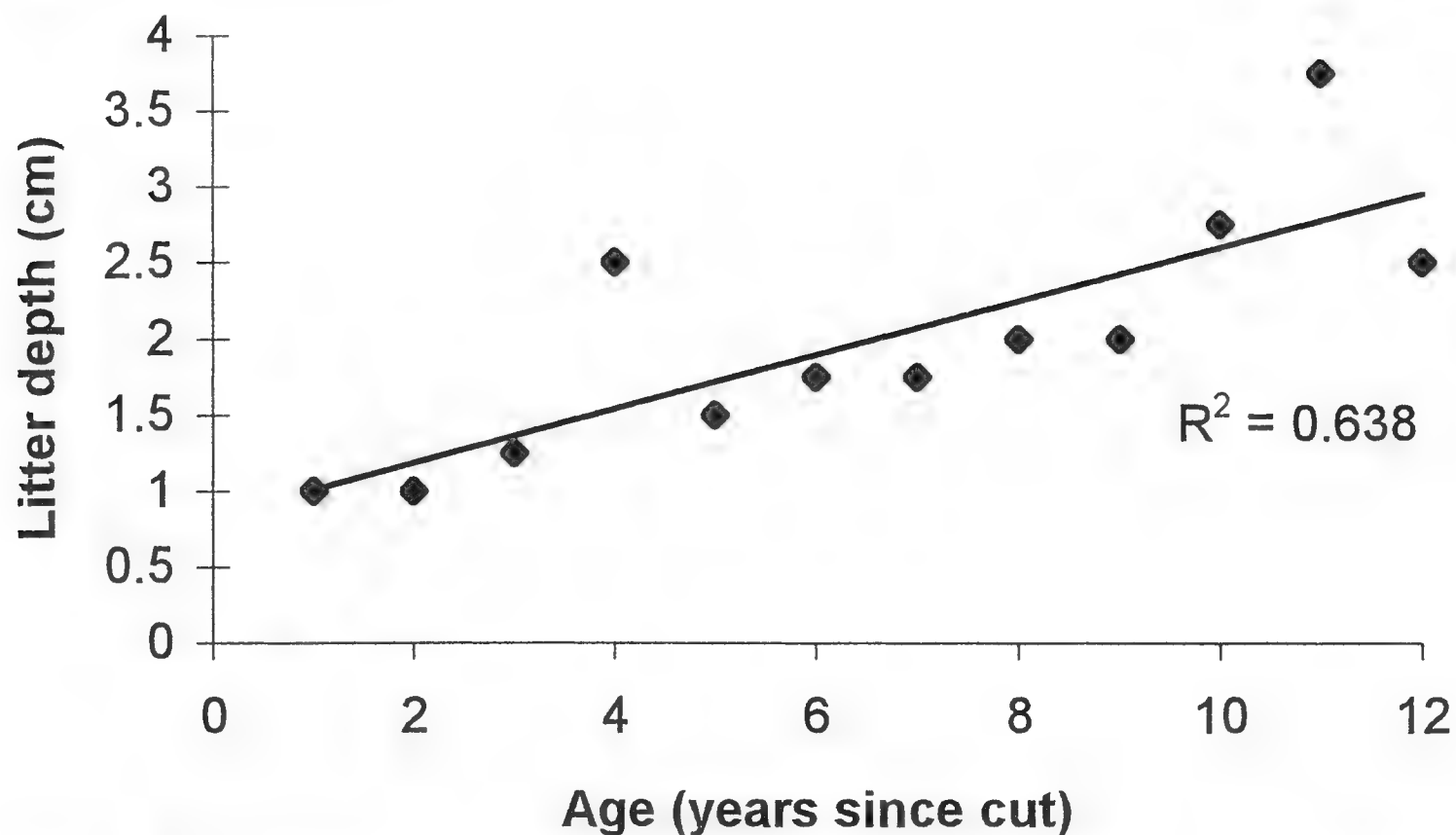
Fig. 2 Relationship between age of coppice compartment and depth of litter.

The overall snail density was found to be 237 live snails/m². Mean densities for individual species are reported in Table 3. As many of the species breed at different times and have different lifespans, their density is likely to change during the course of the year. Certain species are known to have an aggregated distribution (e.g. Mason, 1970) and so the population density for individual compartments (4 samples) is likely to have a greater error margin than the mean for the whole woodland, given in Table 3 which is the result of 56 samples. The proportions of adult and juvenile, live and dead snails of the most abundant species found in the quadrats are given in Table 4. The proportion of live individuals varied, according to species, from 12 to 80% and the juvenile proportion between 15 and 100%.

DIVERSITY

There is a positive correlation of diversity (Shannon-Weaver Diversity Index) with litter cover (p<0.05) suggesting depth and form of litter may be important in determining the composition of the fauna. The diversity is negatively correlated with snail density (p<0.01) and this may reflect the increased dominance of *C. tridentatum* rather than a decrease in general diversity. At high pH, *C. tridentatum* accounts for 80% of the snails.

COMPARTMENT AGE

No linear pattern was observed for snail density in relationship to age of compartment. However, snail density increased for the first 9 years then fell, in years 10 to 12, to just above the 1–3 year (post coppicing) level (Figure 3). In comparison the 40+ year old compartments had a mean density slightly below the mid-cycle peak but above the early and late coppicing levels.

Initial examination of the numbers of each species found alive in the different aged compartments suggested that certain species were not found alive (or in very low numbers) in the compartments most recently cut, i.e. years 1 and 2. This applies to *Acicula fusca, Acanthinula aculeata, Ena obscura, P. pygmaeum* and *V. pellucida*. However, apart from *A. aculeata* this trend is also present in the distribution of dead shells. If this effect had been caused by some environmental factor related to recent coppicing one would expect to have found a similar number of dead shells in year one as the numbers in later years when certain conditions would be similar to the compartment just before it was cut. As this is not the case, other environmental factors may be causing low numbers in these particular species in compartments 1 and 2 and for year 1 at least it implies the low numbers are not due to management.

TABLE 3

Total species found, including density and constancy of those species found in the quadrat samples (D indicates only dead specimens found). The nomenclature used is that given by Walden (1976), except for *Arion distinctus*.

Species	Live Nos/m²	Dead Nos/m²	Total Nos/m²	Constancy % live
Pomatias elegans (Müller)*	5.9	7.4	13.3	32
Acicula fusca (Montagu) *	4.8	4.6	9.4	34
Carychium tridentatum (Risso)**	124.9	138.9	263.9	73
Cochlicopa lubrica (Müller)**	14.5	26.0	40.5	66
Columella aspera (Waldén)	0.3	0.1	0.4	2
Vallonia excentrica (Sterki) D		0.1		
Acanthinula aculeata (Müller)*	4.7	3.7	8.4	48
Ena obscura (Müller)	0.3	1.4	1.7	5
Punctum pygmaeum (Draparnaud)*	6.6	13.0	19.6	53
Discus rotundatus (Müller)**	17.2	53.7	70.9	80
Vitrina pellucida (Müller) *	4.4	5.8	10.1	27
Vitrea crystallina (Müller)	0.1	0.1	0.2	2
Vitrea contracta (Westerlund)**	12.6	17.9	30.4	62
Nesovitrea hammonis (Ström)*	5.1	7.0	12.1	34
Aegopinella pura (Alder)**	11.9	53.7	47.6	59
Aegopinella nitidula (Draparnaud)**	17.4	37.7	55.1	86
Oxychilus draparnaudi (Beck)		0.1		
Oxychilus cellarius (Müller)/sp.	2.6	19.9	22.5	39
Oxychilus alliarius (Müller)	1.3	2.3	3.6	20
Euconulus fulvus (Müller)	0.6	2.7	3.4	7
Cecilioides acicula (Müller)	0.1	0.4	0.5	2
Cochlodina laminata (Montagu)	0.4	1.8	2.1	
Macrogastra rolphii (Turton)				
Clausilia bidentata (Ström)	0.3	0.3	0.6	4
Candidula intersecta (Poiret)				
Monacha cantiana (Montagu)				
Trichia striolata (Pfeiffer) D				
Trichia hispida (Linnaeus)	1.0	7.1	8.1	20
Cepaea nemoralis (Linnaeus)				
Cepaea hortensis (Müller)	0.2	2.7	2.9	5
Helix aspersa (Müller)				
Arion ater ater (agg)				
Arion fasciatus (Nilson)				
Arion hortensis (Férussac)				
Arion intermedius (Normand)				
Arion distinctus (Mabille)				
Milax budapestensis (Hazay)				
Limax cinereoniger (Wolf)				
Limax tenellus (Müller)				
Deroceras reticulatum (Müller)				
TOTALS	237.4	399.3	636.6	

*Those marked ** were represented by over 100 live individuals total and those marked * with numbers between 30 and 100. The rest of the species were represented by fewer than 30 individuals.*
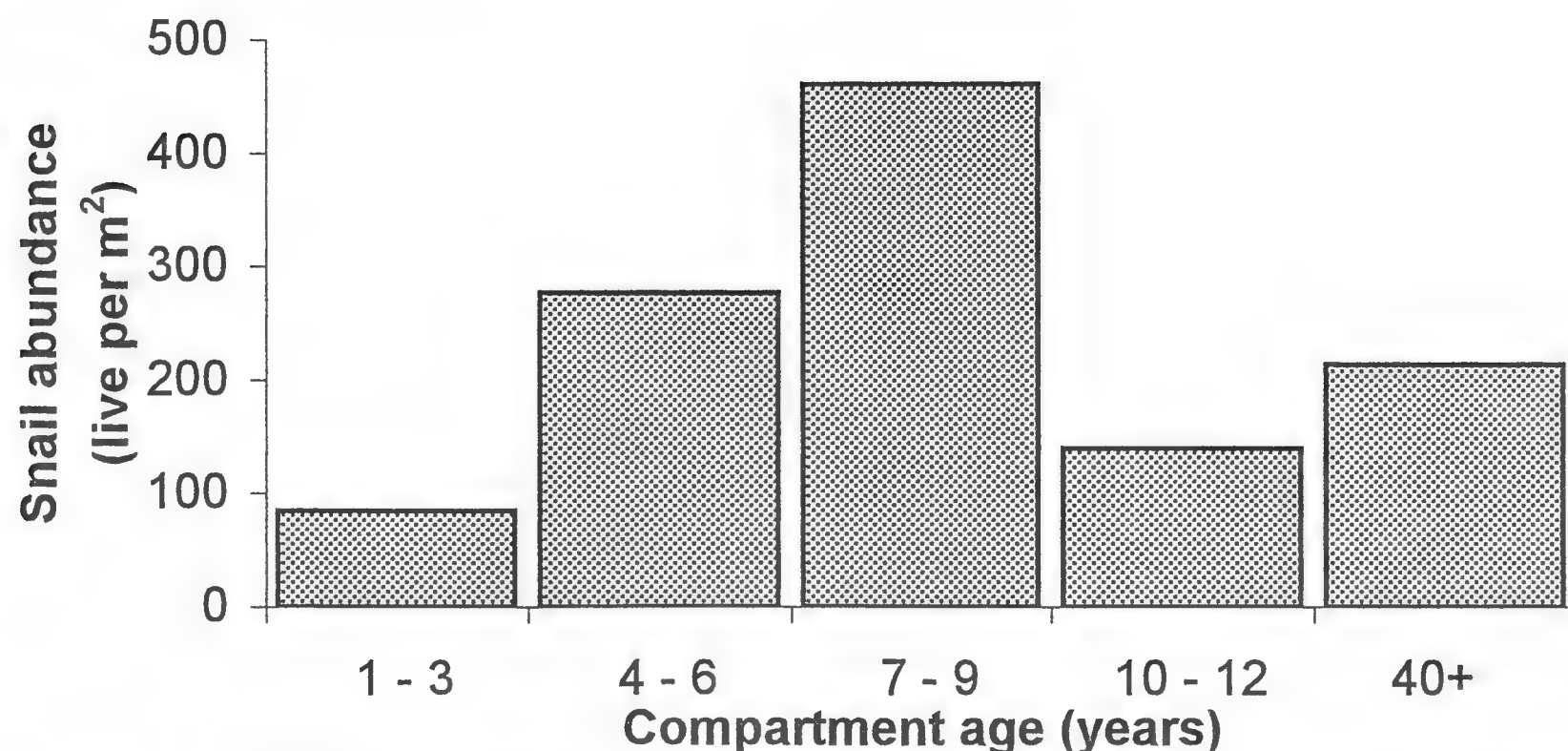
Fig. 3 Relationship between age of coppice compartment and snail abundance.

Further examination suggests that *V. pellucida*, which normally is found only as live juveniles at the time these samples were taken, is found mostly in the first seven years of coppicing. Only very low numbers were found in years 9 and 10 and no live individuals were found in older compartments. Conversely *Oxychilus alliarius* was not found in compartments younger than 4 years and was more abundant in years 10, 11, 12 and 40+. This latter species was found mainly in association with rotting logs and under bark in the general search, and the lack of appropriate logs in the early stages may account for this distribution.

The weighted averages for age are given in Table 5. Species with low age averages such as *P. elegans* tend to occur in young coppice, and conversely *N. hammonis* is at the other extreme in older compartments. The coefficient of variation for each species is relatively large, but species with the largest values such as *A. fusca* and *P. elegans* demonstrate a broad distribution over the compartment ages, and species such as *N. hammonis* and *C. tridentatum* a slightly less broad range.

LITTER

Several species show greater abundance at 2 cm litter depth, notably *Pomatias elegans, Carychium tridentatum, Cochlicopa lubrica, Aegopinella pura, A. nitidula, Discus rotundatus* and *Vitrea contracta* (Table 6). *Punctum pygmaeum* and *Nesovitrea hammonis* increased in abundance up to the maximum litter depth of 4+ cm and *Vitrina pellucida* numbers declined from 1 cm to over 4 cm litter depth. In the one quadrat with zero depth of litter, no live snails were found. The increase in litter depth with compartment age coincides with the increase in recorded density of snails.

PH

All the pH readings from the litter/soil samples were between 4 and 6.8 with a mean of 5.27 (S.E. = 0.093).

Species richness showed a significant positive correlation with pH ($p < 0.05$). Chalk also showed a significant positive correlation with pH ($p < 0.01$). However snail diversity as measured by the Shannon-Weaver Index did not correlate with pH. Similar patterns were observed when analysis was carried out on live, and on dead numbers. Many of the dead snails were clearly no more than one year old; the dead shells were all fresh looking and were found to possess the organic periostracum layer (Cameron & Morgan-Huws, 1975; Evans, 1972). Because of this the analysis was repeated using total species numbers, live and dead. The approximate species number increase per unit pH is 2.3. The inclusion of dead species increases the total species per compartment by an average of 39% (S.E. 4.16%, see Table 1).

TABLE 4
Proportions of live, live juveniles and dead juveniles from the quadrat samples.

Species Name	Total No.	live as % of total	juvenile as % of total live	juvenile as % of total dead
Pomatias elegans	186	80	64	78
Acicula fusca	131	51	31	41
Carychium tridentatum	3694	47	16	25
Cochlicopa lubrica	567	36	77	83
Acanthinula aculeata	118	56	61	52
Punctum pygmaeum	274	34	15	25
Discus rotundatus	983	23	77	76
Vitrina pellucida	142	43	100	83
Vitrea contracta	426	41	86	79
Nesovitrea hammonis	169	42	82	77
Aegopinella pura	619	27	90	87
Aegopinella nitidula	760	30	86	91
Oxychilus sp.	366	15	73	86
Euconulus fulvus	47	19	67	34
Trichia hispida	114	12	71	77
Unidentified	151	13	100	98
Mean		**36**	**68**	**68**

TABLE 5
Weighted averages for pH and age. t = weighted standard deviation, CV = Coefficient of variation

Age 1-12 years	Age	percent	t	CV
Pomatias elegans	4.6	0	2.76	60.0
Acicula fusca	4.9	9.7	3.78	77.1
Vitrina pellucida	5.2	19.4	2.02	38.8
Aegopinella nitidula	5.5	29.0	3.09	56.2
Aegopinella pura	5.6	32.2	2.84	50.7
Discus rotundatus	5.9	41.9	3.03	51.4
Oxychilus cellarius/sp	6.2	51.6	2.95	47.6
Vitrea contracta	6.1	48.4	2.48	40.6
Acanthinula aculeata	6.4	58.0	2.92	45.6
Carychium tridentatum	6.6	64.5	2.47	37.4
Cochlicopa lubrica	6.8	71.0	2.63	38.7
Punctum pygmaeum	6.8	71.0	2.99	44.0
Nesovitrea hammonis	7.7	100	2.62	34.0
Weighted Av. pH	**pH**			
Nesovitrea hammonis	4.6	0	0.41	8.8
Acicula fusca	4.8	13.3	0.53	11.1
Punctum pygmaeum	5.1	33.3	0.71	13.9
Aegopinella nitidula	5.4	53.3	0.68	12.6
Oxychilus cellarius/sp	5.4	53.3	0.83	15.4
Acanthinula aculeata	5.4	53.3	0.66	12.2
Discus rotundatus	5.5	60.0	0.69	12.5
Cochlicopa lubrica	5.6	66.7	0.55	9.8
Vitrea contracta	5.7	73.3	0.46	8.1
Aegopinella pura	5.8	80.0	0.62	10.7
Carychium tridentatum	5.9	86.7	0.50	8.5
Vitrina pellucida	6.0	93.3	0.63	10.4
Pomatias elegans	6.1	100	0.37	6.0
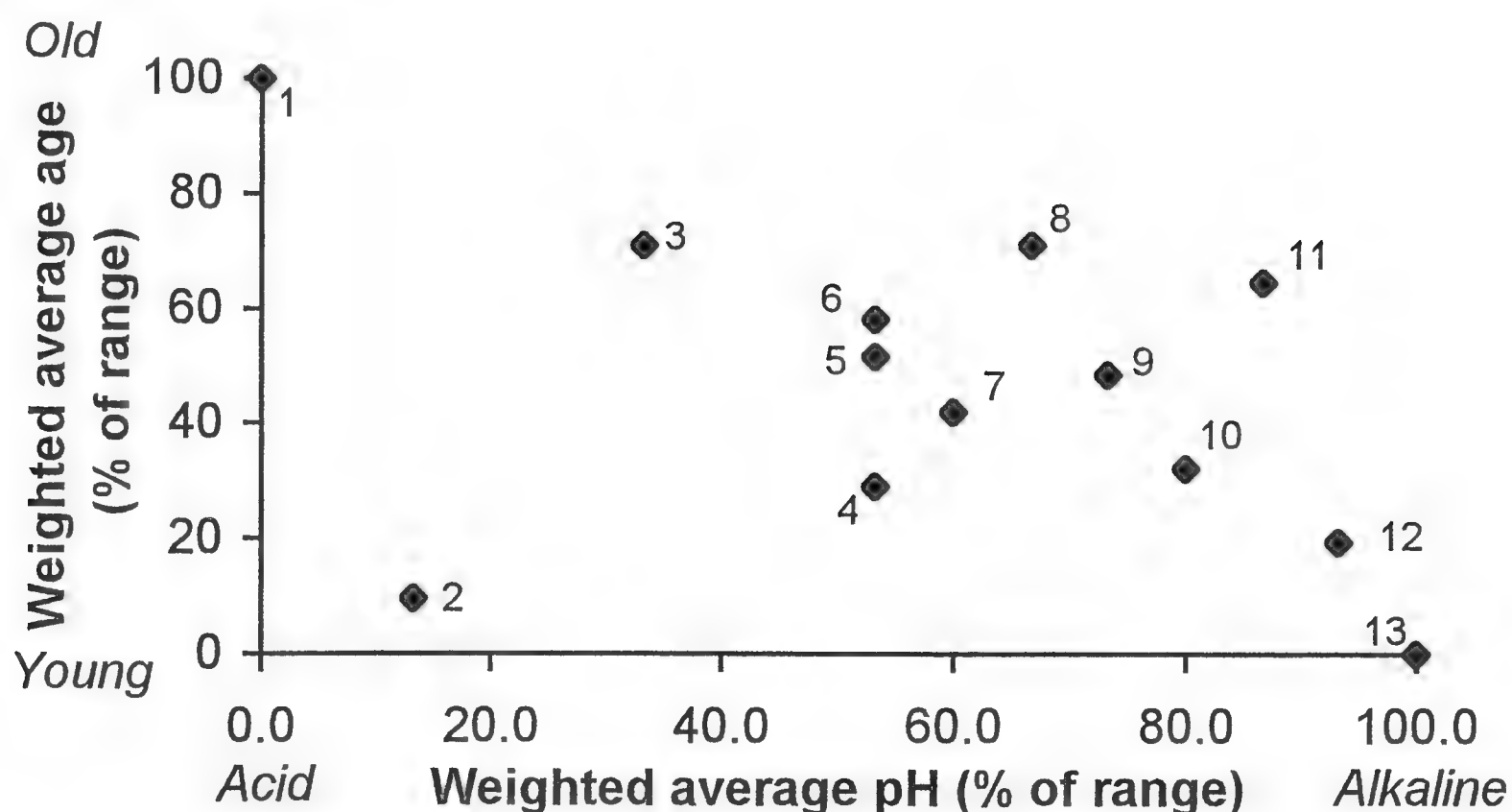
Fig. 4   Relationship between weighted average pH and age. **1** *N. hammonis* **2** *A. fusca* **3** *P. pygmaeum* **4** *A. nitidula* **5** *O.* sp. **6** *A. aculeata* **7** *D. rotundatus* **8** *C. lubrica* **9** *V. contracta* **10** *A. pura* **11** *C. tridentatum* **12** *V. pellucida* **13** *P. elegans*.
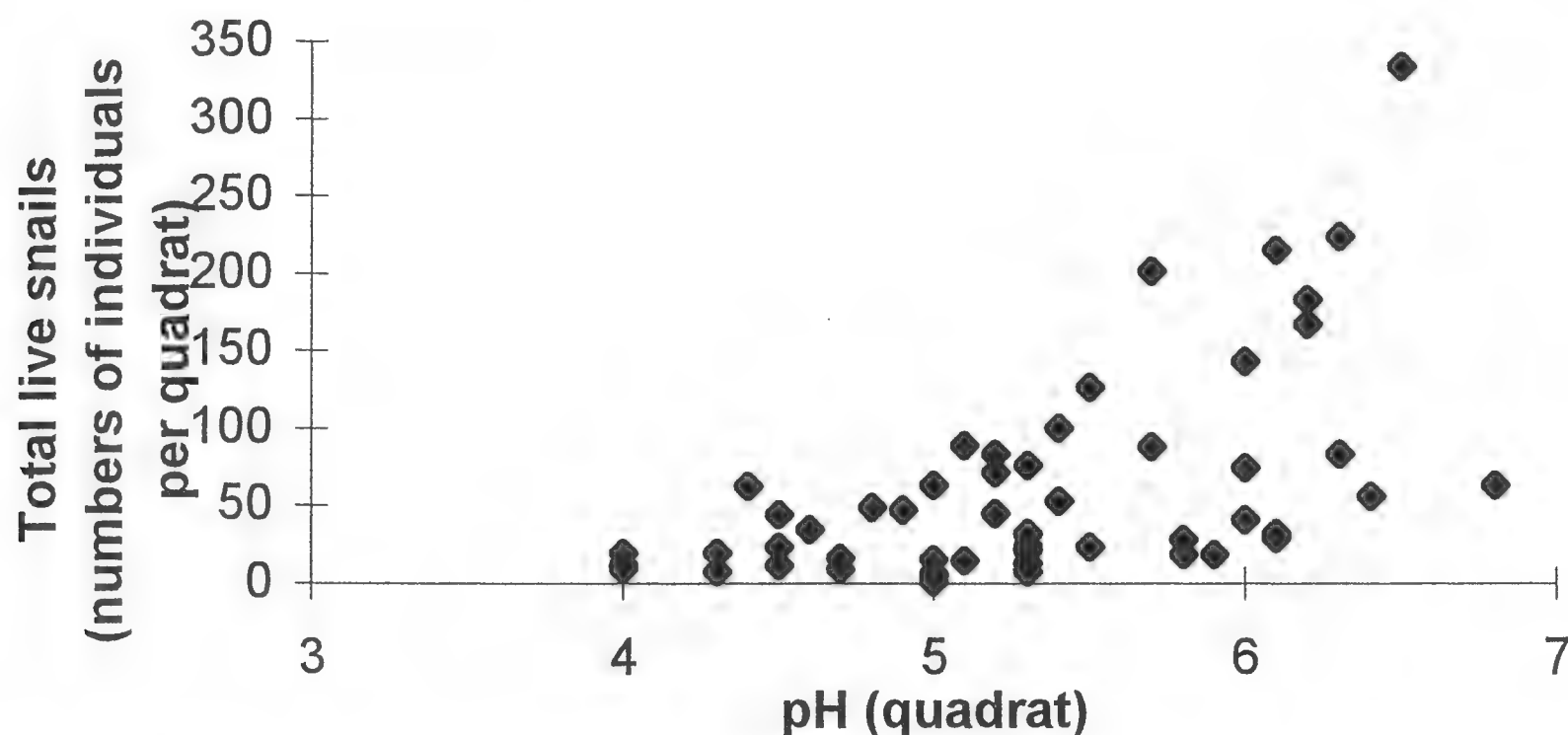
Fig. 5   Relationship between pH and total number of live snails per quadrat.

The weighted averages for pH (Table 5) indicate that species such as *N. hammonis* and *A. fusca* tend to be more common at lower pH and conversely that *P. elegans*, *V. pellucida* and *C. tridentatum* are more abundant at the higher pH range. The coefficient of variation is much smaller than that for age, for each of the species, and the most restricted species are seen to be *P. elegans* and *Vitrea contracta*. Only three species showed a lower threshold pH value. These were *P. elegans;* which was not found at pH below 5.2, and *C. tridentatum* and *C. lubrica* not found below 4.5. An upper threshold for *N. hammonis* was found to be 6.0. Figure 4, of percentage weighted average of age against pH, enables a greater separation to be achieved with regard to pH but little difference between age.

No correlation was found with pH or chalk and total snail density. However, inspection of the data indicates that the maximum number of live snails does increase with chalk and pH (Figure 5). Failure to find a correlation is due to the fact that at any one pH some quadrats have low numbers or no snails and this paucity is due to factors other than pH.

When the mean abundance of individual species per compartment was examined only *V. contracta* showed a strong positive correlation with pH (p<0.001). However, when the pH is divided into 6 ranges (4–4.4, 4.5–4.9, 5.0–5.4, 5.5–5.9, 6.0–6.4, 6.5–6.9) and plotted against mean abundance for individual species for the 56 quadrats some interesting relationships emerge:

TABLE 6

Mean snail abundance (per m²) at different litter depths (in bold). (In brackets: Standard Error. Below: percentage of total per species).

Litter depth	0 cm	1 cm	2 cm	3 cm	4+ cm
Number of Quadrats	**1**	**18**	**23**	**10**	**4**
Pomatias elegans	0	**3.1** (2.0)	**11.1** (4.2)	0	**5.0** (5.0)
		17	58		25
Acicula fusca	0	**2.0** (1.0)	**3.6** (1.9)	**12.0** (6.3)	**7.0** (4.1)
		8	15	49	28
Carychium tridentatum	0	**41.6** (15.2)	**237.7** (61.1)	**60.4** (34.0)	**44.0** (28.6)
		11	62	16	11
Cochlicopa lubrica	0	**10.2** (3.5)	**20.7** (5.1)	**12.8** (5.1)	**6.0** (6.0)
		20	42	26	12
Acanthinula aculeata	0	**4.0** (1.3)	**5.0** (1.4)	**4.8** (2.1)	**7.0** (4.7)
		19	25	23	33
Punctum pygmaeum	0	**2.7** (0.9)	**8.0** (2.1)	**6.8** (2.7)	**17.0** (14.4)
		8	23	20	49
Discus rotundatus	0	**14.0** (3.6)	**20.7** (4.0)	**14.0** (6.2)	**14.0** (2.6)
		22	33	23	22
Vitrina pellucida	0	**7.1** (3.2)	**4.2** (1.8)	**1.2** (1.2)	**2.0** (2.0)
		46	30	9	15
Vitrea contracta	0	**4.4** (2.4)	**21.2** (3.9)	**9.6** (4.5)	**10.0** (8.7)
		10	47	21	22
Nesovitrea hammonis	0	**3.1** (1.6)	**3.1** (1.1)	**4.8** (3.1)	**27.0** (27)
		8	8	13	71
Aegopinella pura	0	**8.9** (3.1)	**17.0** (3.9)	**10.4** (4.3)	**2.0** (2)
		23	45	27	5
Aegopinella nitidula	0	**11.3** (2.2)	**20.5** (3.3)	**17.2** (2.3)	**20.0** (3.6)
		16	30	25	29
Oxychilus sp.	0	**3.8** (1.1)	**3.1** (0.9)	**6.0** (1.9)	**5.0** (3.8)
		31	33	27	9

1 *D. rotundatus, A. pura, V. contracta, P. elegans* and *V. pellucida* become more abundant with increasing pH. *C. lubrica* and *A. nitidula* increase initially but decline at higher pH (above pH 6.0). *C. tridentatum* increases greatly with pH (Table 7).

2 *A. aculeata* and *Oxychilus* sp. show no pronounced trend. *A. fusca* also shows little trend but is more abundant at pH range 4.5–4.9 (Table 7).

3 *N. hammonis* declined in abundance with increasing pH and *P. pygmaeum* also initially, before levelling off (Table 7).

CHALK

As with pH, *P. elegans, C. tridentatum, V. pellucida* and *V. contracta* tended to increase in abundance with free chalk, and *P. pygmaeum* and *N. hammonis* tended to decrease.

There is a small geographical connection between the distribution of free chalk and the location of compartments. Those with higher measurements of free chalk lie in the south and west and those with least, including the two compartments with no free chalk, lie in the north and east. This is likely to be linked to the depth of Head deposits

TABLE 7
Mean snail abundance (per m²) at different pH ranges (bold). (In brackets: Standard Error.
Below: percentage of total per species.) Data for species with numbers over 30.

pH range	4.0–4.4	4.5–4.9	5.0–5.4	5.5–5.9	6.0–6.4	6.5–6.9
No.of Quadrats	6	11	19	7	11	2
P. elegans	0	0	1.4 (1 1)	4.6 (1.8)	20.4 (7.8)	20.0 (20)
			11	10	67	12
A. fusca	2.0 (2.0)	14.2 (6.1)	3.9 (1.6)	0.6 (0.6)	1.8 (1.2)	0
	4	59	29	1	7	
C. tridentatum	0	26.5 (9.4)	69.9 (21.0)	170.9 (69.4)	282.9 (82.8)	534 (535)
		4	19	17	45	15
C. lubrica	0	9.45 (4.4)	12.8 (3.5)	22.3 (13.9)	25.8 (5.4)	12.0 (4.0)
		13	30	19	35	3
A. aculeata	2.0 (1.4)	5.1 (1.8)	4.2 (1.4)	7.4 (3.5)	3.3 (1.5)	13.0 (2.7)
	4	21	30	20	14	11
P. pygmaeum	15.3 (9.2)	9.8 (4.0)	4.0 (1.5)	3.4 (2.2)	4.8 (1.4)	6.0 (6.0)
	25	29	21	6	15	3
D. rotundatus	8.7 (3.3)	10.5 (3.4)	13.9 (3.2)	23.4 (7.8)	20.4 (6.1)	52.0 (20.0)
	5	12	28	18	24	11
V. pellucida	0.7 (0.7)	0.4 (0.4)	3.2 (2.0)	2.3 (1.5)	10.2 (3.4)	24.0 (24.0)
	1	1	25	7	46	20
V. contracta	5.3 (4.0)	3.6 (1.8)	10.5 (3.1)	13.1 (8.4)	22.5 (5.8)	46.0 (6.0)
	5	6	28	13	35	13
N. hammonis	25.0 (16.7)	6.5 (2.7)	2.7 (1.7)	0.6 (0.6)	0.4 (0.4)	0
	54	25	18	1	1	
A. pura	4.0 (1.8)	2.2 (1.1)	8.6 (2.6)	10.9 (3.6)	25.8 (6.3)	46.0 (2.0)
	4	4	25	11	43	14
A. nitidula	10.7 (3.5)	15.6 (3.6)	14.3 (2.8)	16.6 (3.2)	24.4 (5.2)	18.0 (2.0)
	7	18	29	12	29	4
Oxychilus sp.	6.7 (3.0)	4.4 (1.5)	2.3 (0.6)	3.4 (1.4)	4.0 (1.6)	10.0 (10.0)
	18	22	20	11	20	9

and the soil formed on it. This distribution did not appear to be obviously reflected in snail density or diversity.

VEGETATION COVER

Initial inspection of data did not reveal any obvious relationships or significant correlations however, *Oxychilus cellarius* was not found in quadrats with more than 50% moss cover and although generally of low density, its mean abundance was twice as high at the 0–25% moss cover than it was at the 26–50% moss cover. *Vitrina pellucida* was not found in quadrats with less than 45% vegetation cover.

DISCUSSION

GENERAL

Most sampling methods are biased to a certain degree. Quadrat sampling, of the sort used here, gives good representation of fauna in the soil, litter and lower vegetation but will under-represent species which have strong microhabitat preferences not found within the quadrat, such as those with arboreal or dead wood preferences. Very few

slugs were found alive in the quadrats. Thus, only those species commonly found on the ground in leaf litter will show realistic population densities. *Cecilioides acicula* lives in the soil and has been found alive 1.5 m below the surface (Evans, 1972) so surface soil and litter samples will not represent it accurately. Similarly, those species, such as *Macrogastra rolphii, Clausilia bidentata* and *Cochlodina laminata,* commonly found in trees or log piles, will be poorly represented. The most favourable areas for finding snails, particularly those species rarely found in the soil sample, were around and under the bark of rotten logs, tree trunks, and under clumps of butcher's broom (*Ruscus aculeatus*) in the most recently coppiced compartment.

SPECIES RICHNESS

The 38 species (including 9 slugs, but excluding the single *Vallonia* and *Candidula*) found at West Dean Woods Nature Reserve may be compared with other studies. Wardhaugh (1996b) compared species richness from investigations in woodlands in the British Isles and found a range of species number per wood of between 4 and 39 in the British Isles.

Compared with other coppice sites, West Dean Woods Nature Reserve would appear to be quite rich. Berry (1973) found only five species from coppice plots within a woodland where he found 16 out of a known 30 terrestrial molluscs. Reynolds (1993) found only 14 species at the coppiced site out of a known 43 to have been recorded from the Loder valley as a whole, and Paul (1978) recorded 26 species from coppice plots of different ages. However, four such studies, each using different methods, are insufficient upon which to base any conclusions.

SNAIL DENSITY

The figure of 237 live snails/m² (not including slugs) may be compared with a few other quantitative studies, such as Mason (1970) who found 489/m² in Wytham woods (beech woodland) near Oxford and 1085/m² in less exposed beech woods there. Other studies elsewhere in Europe (details in Mason, 1974 and Bishop, 1977a) have produced numbers of between less than 100/m² to well over 1000/m². Mason (1970) gives details of the density of individual species of snails living in beech litter and the species common to both his study and the present study have very different densities. Both Mason and the present study found that *Carychium tridentatum* was the most abundant. Mason found the next most abundant to be *Acanthinula aculeata, Punctum pygmaeum, Oxychilus* spp. (*cellarius* and *alliarius* combined), *Vitrea contracta* and *Aegopinella pura.* In the present study the order of abundance was *C. tridentatum, A. nitidula, Discus rotundatus, Cochlicopa lubrica, Vitrea contracta* and then *A. pura.*

Comparison between the quadrat constancy (Table 1) and species density (Table 2) gives an insight into the distribution of the species. For example *C. tridentatum,* the most abundant at 124.9/m², and known to aggregate, was found in only 73% of the quadrats whereas *Discus rotundatus* and *A. nitidula,* only one seventh as abundant, occurred in 80% and 86% respectively. Conversely, *Acicula fusca* and *Acanthinula aculeata* have approximately the same density (4.8 and 4.7/m²) yet their constancy was 34% and 48% suggesting a certain degree of clumping for *A. fusca,* which was apparent from the samples.

SPECIES DIVERSITY

The negative correlation found between snail diversity (Shannon-Weaver Diversity Index H) and snail abundance (square root of total live numbers) (p<0.01) is of interest. This suggests that as total snail abundance increases the community becomes dominated by a limited number of species, particularly *Carychium tridentatum.* The decrease in diversity might result from competition. Boycott (1934) believed that intraspecific competition between snails was a negligible factor (but that interspecific competition

may account for some of the difference in *Cepaea* sp. distribution), and that 'food has no influence either by its quality or quantity on the recurrence [sic] of our land Mollusca'. Molluscs certainly seem to take a variety of different foods, but Carter, Jeffery & Williamson (1979) suggest that 'good quality' food may be limiting at certain times of year. Tilling (1985a, 1985b) produces evidence for both intra- and inter-specific competition for *Cepaea*. Cook and Cain (1980) refer to suggestions of chemical inhibition by Williamson *et al.* (1976), and to predator-deterrent chemicals in the mucus trail of some species of slug by Oosterhoff (1977). These could adversely affect other mollusc species when density is high. Waldén (1981) considered that when conditions were optimal, species tended to accumulate rather than replace each other, and that competition was negligible in northern woodland. In this study the number of species also increases with increased abundance. However, it would appear that some sort of competition is occurring, although whether it is mainly intra- or interspecific is not at this stage clear and warrants further research.

Using previously published data, the Shannon-Weaver Diversity Index (H) was calculated from five studies.

Valovirta (1968) Finland, woodland on alkaline igneous rocks.

H	1.45	1.67	2.11	2.13
pH (midrange)	5.0	5.8	6.3	7.0
nos/litre	126	172	229	203

Wareborn (1969) Sweden, various woodlands on acid igneous rock.

H	2.39	1.74	1.99	2.1	1.9	1.04	2.05	1.89	1.87	1.79	2.09	2.19
pH	5.5	6.3	5.8	6.5	6.3	6.5	5.0	5.8	4.8	8.0	5.7	7.0
nos/3 1	205	1191	505	308	463	1685	352	568	95	910	673	656

Wareborn (1970) Sweden, variety of woodlands on acid igneous rock.

H	1.49	2.27	2.34	2.45
pH	4.5	5.0	6.0	6.5
nos/3 1	68	152.5	520.6	627.7

Waldén (1981) Sweden, wooded talus and boulder slope, on acid igneous rock.

H	1.68	1.75	1.73	2.27	2.18	1.94	2.53	2.1	2.36	2.35
pH	5.25	4.5	5.5	7.25	6.2	6.0	6.8	7.5	7.25	7.0
nos/20 1	478	64	346	543	2167	548	469	1068	1783	2197

Gardenfors (1992) Sweden, 80–100 year old beech forest, artificially limed.

H	1.44	0.53	1.11	1.04
pH	4.67	5.07	5.4	6.26
nos/m²	50	480	325	1138

Of these, Wareborn (1969) and Gardenfors (1992) were the only ones to show similar trends to those found in this study, i.e. Diversity (H) showing an inverse relationship with snail abundance and no particular relationship with pH (Figure 6). Wareborn found that *Punctum pygmaeum* and *Carychium tridentatum* became dominant at high density, and Gardenfors' data suggests *P. pygmaeum* became dominant (*C. tridentatum* was not present). In our study only *C. tridentatum* became dominant. Of the remaining three studies for which Diversity (H) was calculated, Waldén (1981), Wareborn (1970) and Valovirta (1968) showed that H increased both with abundance and pH.
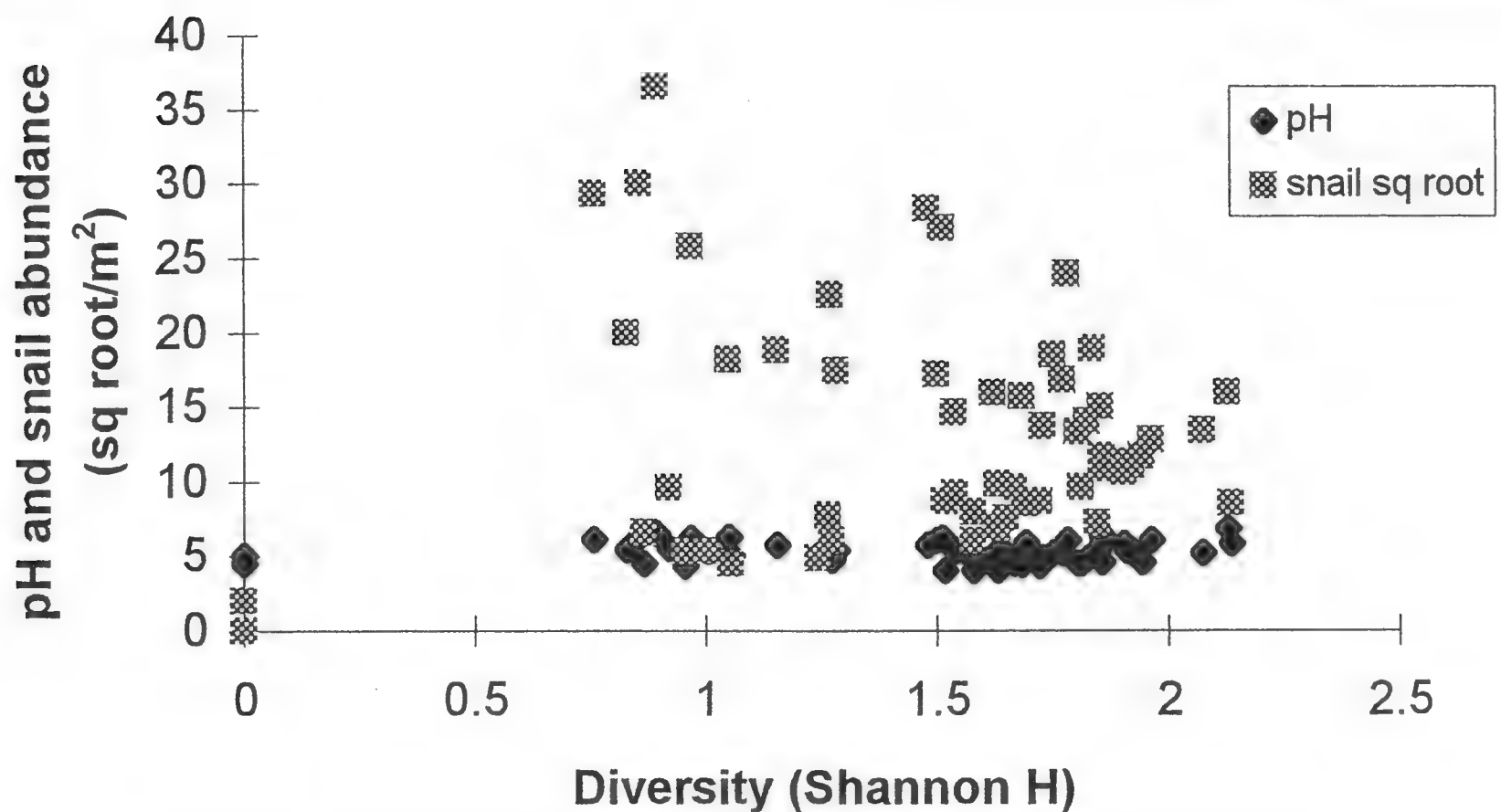
Fig. 6   Relationship of pH and abundance with Diversity.

PROPORTION OF JUVENILES AND DEAD

The mean proportion of live juveniles to the total live snails was 68% and dead juveniles to total dead was also 68%. Boycott (1934) considered that the principal mortality of land molluscs fell on the juveniles, this being probably due to predation or desiccation. Most of the species listed on Table 4 have higher or lower proportions than 68%. Lack of adequate data on the ecology and life-cycles of these species makes it difficult to do more than list the possible reasons.

Possible reasons for low proportions of juveniles are:

1 The method of extraction may enable the youngest juveniles of the smallest species (e.g. *Punctum pygmaeum* and *Carychium tridentatum*) to be lost through the 0.5 mm sieve. The protoconchs of *C. tridentatum* measure 0.43 x 0.31 mm so could be lost easily.

2 Some of the youngest juveniles were difficult to allocate to species level, for example the Zonitidae. Unidentifiable juveniles accounted for 2.3% of the dead snails and 0.6% the Zonitidae. If all were identified, this would have the effect of making the Zonitidae juvenile proportions even higher (already between 76% and 91% juvenile).

3 If few eggs are laid in early spring, or if low numbers are laid throughout the year then low numbers of juveniles will occur in these samples. Morton (1955) suggests that the maximum egg laying period for *C. tridentatum* from Box Hill in Surrey is June, although some egg laying takes place throughout the year. This could account for the low proportion of live juveniles (16%). However, Bulman (1990) who reared Polish *C. tridentatum* in the laboratory found that March to May was one of three main egg laying (and hence hatching) periods.

Possible reasons for high proportions of young may be:

1 Recently hatched young snails. There were abundant juvenile Zonitidae in some samples. If eggs are laid in large batches, one or two of these, recently hatched, would raise the proportion of juveniles, especially if the adults were not particularly abundant, as in the case of *Oxychilus cellarius*.

2 An annual life cycle from spring to spring would result in few adults and abundant juveniles at the time the samples were taken. *Vitrina pellucida*, which were found alive only as juveniles, are believed to lay eggs in March and early April and all the adults then die and juveniles appear in May (Paul, 1975). The present findings support this.

The mean proportion of live to dead shells found in this wood is 36%, and is a reflection of the such factors as population dynamics and persistence of empty shells. *Pomatias elegans,* which has probably the thickest and most persistent shell of the species found, had the highest proportion of live animals. The reason for this is unknown. No similar studies have been located with which to compare this population structure data and it would benefit from further research.

pH

Correlations and graphical relationships cannot be taken to mean that the factors are linked directly. However, the results clearly show that pH and litter have some effect on the abundance of snails, but that there is no apparent direct relationship with the coppicing. Factors affecting soil pH are many, for example; the proportion and type of leaf litter, recent rain, whether oven dried or air dried and length of time between collection and testing (Russell, 1988; Turner, 1958 (in Smith, 1980); Valovirta, 1968).

Due to the complexity of measuring pH, care must be taken when comparing absolute values between studies. Gardenfors (1992), Outeiro *et al.* (1993) and Valovirta (1968), looked at litter pH. Bishop (1980), Cameron (1973) and Wareborn (1969) looked at the relationship between snails and soil pH. Ovington & Madgwick (1957, in Williams & Gray, 1974) and Hermida *et al.* (1995a) found a broad correlation between the soil pH and that of the tree leaves and litter, so it may be that the combined soil/litter pH gives a more realistic measure of the mean pH the snails experience. However, Frankland *et al.* (1963) found litter and vegetation pH similar but soil pH differed considerably.

We found a positive correlation between pH and the visual assessment of chalk ($CaCO_3$) content to $p < 0.01$. Although pH is not believed to be closely correlated to calcium content, there is a link between the two which depends upon solubility of carbonates (e.g. $CaCO_3$), and partial pressure of CO_2. The pH is likely to give an approximate indication of the calcium availability (Cameron, 1973). However, Frankland *et al.* (1963) found no correlation between calcium ion content and pH in two oakwoods but did find one in a larch wood.

In this study we found that pH correlated with snail species richness ($p < 0.05$) (but only to $p < 0.1$ with square root of total snail abundance), but relationships were found between pH and individual species. Bishop (1976), Cameron (1973, 1978), Valovirta (1968) and Wareborn (1970), found a correlation between soil pH and snail numbers, and Hermida *et al.* (1995a & b) found a correlation between soil pH and snail distribution. Gardenfors (1992) and Outeiro *et al.* (1993) found the pH of the litter to be important to snails. However, Tattersfield (1990) found that mean soil pH did not correlate significantly with mollusc richness or abundance. Figure 7, of pH against species richness, indicates a correlation nearly as strong as Waldén's (1981) for wooded taluses and boulder slopes. The approximate total species numbers increase per unit pH is 2.3. (The graph and species number for live is similar.) Waldén found a 5 species increase per pH unit. Cameron (1973) found a significant positive correlation between species number and pH with an increase of between 4.7 and 2.9 species per unit pH increase.

Regarding the relationship of individual species to pH, Waldén (1981) also found *Nesovitrea hammonis* to have its optimum at low pH and low numbers or absent at higher pH. Several studies have found *Punctum pygmaeum* and *N. hammonis* to be acid tolerant (e.g. Cameron, 1973; Hermida *et al.,* 1995a; Paul, 1975; Waldén, 1981; Wareborn, 1970). We found similar patterns in this study, with weighted averages for *N. hammonis, Acicula fusca* and *P. pygmaeum* the most acid. *Vitrina pellucida* and *Pomatias elegans* had the most alkaline weighted averages. However, Gardenfors (1992) found *P. pygmaeum* and *N. hammonis* to have a positive relationship with pH, with *P. pygmaeum* numbers increasing 40 fold with the addition of lime. It could be that *P. pygmaeum* is tolerant of a broad pH range. The importance of pH for molluscs is not well understood, but may be partly
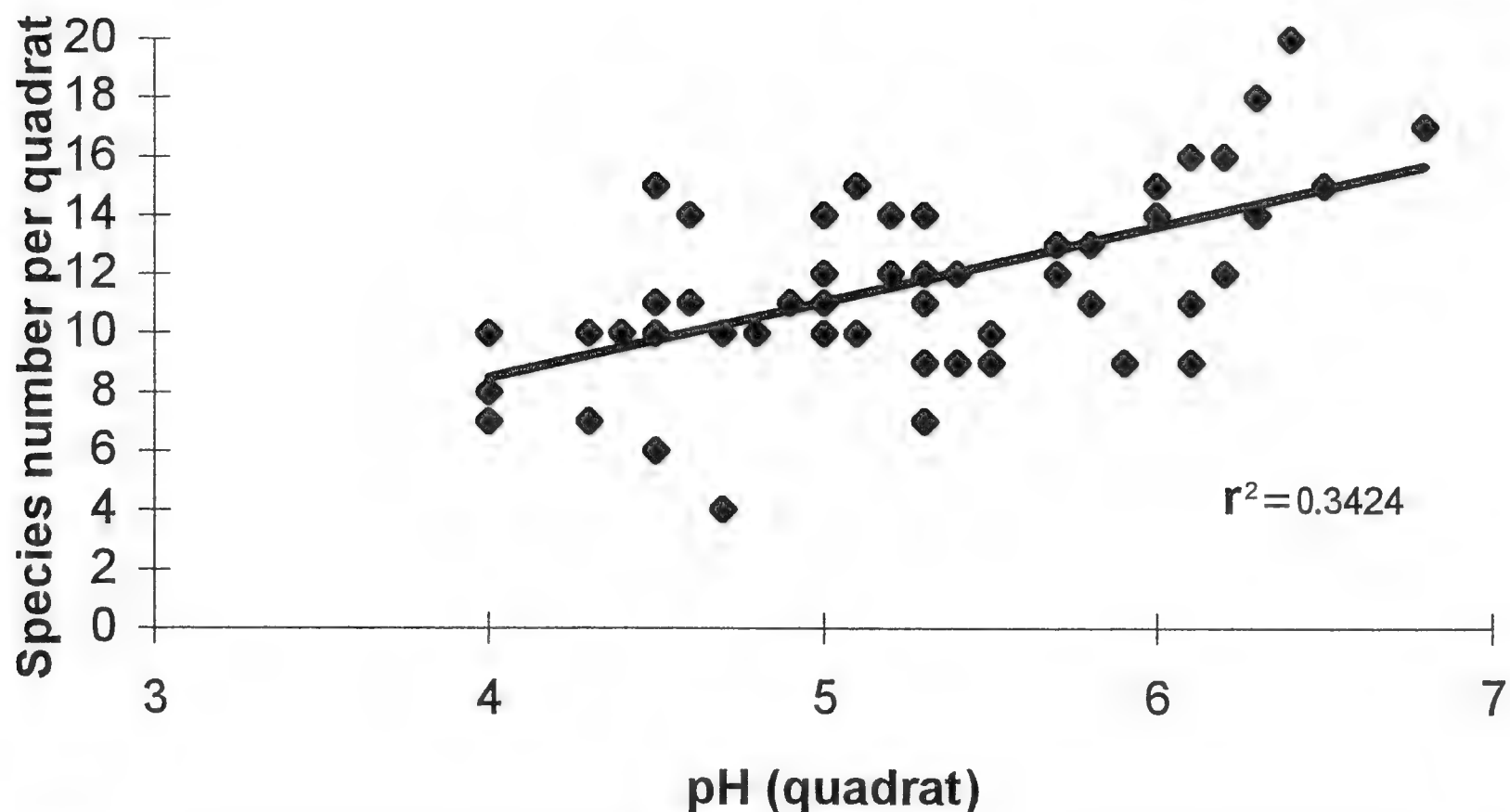
Fig. 7   Relationship between total species number and pH of quadrats.

due to the crude relationship which pH has with calcium which is known to be of importance to snails.

Despite the lack of significant correlation there is a clear link between pH and number of live individuals (Figure 5). This illustrates the importance of combining visual inspection of the data with statistical analysis. Low numbers can be found at high pH, suggesting that the presence of high pH enables the potential for high numbers of snails to occur, providing other environmental conditions are also met and there is not another factor limiting increase in numbers. Age and other measured variables did not account for this pattern. Preliminary analysis suggests soil texture may be a key factor limiting numbers in high pH sites.

LITTER

Our results indicate that there is a clear link between snails and litter. Many of the snail species showed greater abundance in quadrats with 2 cm deep litter. Two species (*Punctum pygmaeum*, *Nesovitrea hammonis*) showed increasing abundance with litter depth. Only *Vitrina pellucida* showed a decline in abundance with litter depth. A relationship was found between litter cover and snail diversity. Berry (1973) found that snails were associated with litter patches in recent coppiced woodlands. This, he believed, was due more to textural, mechanical and moisture retention reasons than food, even though litter is considered to be the main food of many small woodland snails (Mason, 1970). Paul (1975) found few molluscs in areas where there were accumulations of leaves (and sparse ground flora) which he attributes to reduced pH but gives no indication of relative litter depth. Cameron (1978) found soil and litter dwellers on limestone pavement were reduced when grazing caused reduction in loose soil and litter.

The late spring is the seasonal minimum of tree litter density (Sydes & Grime, 1981). Barkham (1992) considers that there is a rapid disappearance of litter in the open phase of coppicing with maximum wind-sorting and redistribution, with litter rising as shade increased. The first year would see little input to the litter and normal or slightly enhanced decay would continue, resulting in a great reduction of the litter layer. As the coppice stools regrow and the ground flora flourishes litter input would increase rapidly. The soft vegetation of the ground flora, favoured by invertebrates, is likely to decay or be eaten rapidly, and the tree leaves will be the main contributors to the litter build up. The litter depth in high deciduous forest on mull soil probably reaches an equilibrium level and is likely to be fairly stable. The litter depth in the 40+ year compart-

ments suggests a similar occurrence in coppice woodlands given sufficient time. Ovington (1953) and Barkham (1992) both consider a mature woodland probably achieves a balance between litter input and decomposition, except where waterlogged or acid. Litter is frequently acidic (Williams & Gray 1974) and, therefore, could cause a slightly lower pH. There are a range of opinions as to the degree to which the litter and vegetation affect the soil pH (e.g. Wareborn, 1969, 1970; Williams & Gray, 1974). Certain snails tolerate a soil of low pH if the litter (foerna) (leaf mould layer, Valovirta 1968) is of a base rich type (Wareborn, 1970). No significant correlation between litter depth and pH was found in this study. However, it was apparent that pH varies at different litter depths.

Litter depth/cm	0	1	2	3	4+
Mean pH	4.5	5.4	5.4	4.9	4.9
Standard error	0	0.17	0.16	0.16	0.2

All the quadrats with litter depths of 3 cm and over had pH of less than 5.5 and only one of the 14 quadrats with 3 cm litter or more had any free chalk. This could be interpreted as litter causing a reduction in the pH. Alternatively, absence of chalk, or low pH, may cause less favourable conditions for decomposers thus reducing the rate of litter decomposition and allowing accumulation. The earthworms (as measured by worm granules, and to be published elsewhere) which are the most important organisms in leaf litter decomposition, were found to be correlated strongly with pH and chalk (both $p < 0.001$). There is a complicated relationship between snails, pH, calcium and worm activity which warrants further research.

CHALK

Snails are believed to have a close relationship with the calcium content of the litter and soil (Bishop, 1977a; Burch, 1955; Hermida *et al.*, 1995a, b; Lozek, 1962; Outeiro *et al.*, 1993; Valovirta, 1968). Calcium is required for their shells and various reproductive and metabolic functions (e.g. Wareborn, 1970, 1992). Soluble calcium ions tend to be absorbed in the humus and uppermost layers of soil thus forming a favourable environment for snails even in an apparently acid soil (Valovirta, 1968). Hazel *(Corylus)* was present all over the site and has a moderate calcium citrate content (Valovirta, 1968). Ash *(Fraxinus)*, with a high calcium citrate content, was also present in places. Calcium oxalate is the dominant calcium salt in oak leaves but has a much smaller pH-increasing effect than calcium citrate (Wareborn, 1970). In spite of the coarse method of assessment of calcium used (subjective assessment of chalk particles in the sample) several species showed relationships with abundance of chalk, in a similar way to that of the pH measurements.

VEGETATION

The increase in vegetation in the early years of coppicing did not appear to have any measurable effect on the snail fauna. We were unable to find any indication whether or not the vegetation compensated for reduction of litter or ameliorated the presumed increases in temperature variation, exposure, humidity reduction etc. associated with early coppice stages. Live plants are not believed to be a very important part of the diet of the most frequently found species in this wood. Only one species *(Vitrina pellucida)* showed a threshold value of 45% vegetation cover, below which it was not found, and *Oxychilus cellarius* was not found in quadrats with a moss cover greater than 40%.

COMMENTS ON SPECIES

Vitrea crystallina was rare in this woodland. It is considered to be a hygrophilous species by Wareborn (1970) and Paul (1975) and catholic, but favouring damp places, by Kerney

& Cameron (1979) which may account for its virtual absence in this relatively dry woodland. It is possible that the exposure to drier conditions and temperature fluctuations after coppicing are adverse to its survival, but surprisingly its only live occurrence was in the compartment which had just been coppiced. Reynolds (1993) did not find *V. crystallina* in her coppice site, however Paul (1978) found this species in the wetter Hayley Wood coppice sites. Neither found *V. contracta* which was abundant in West Dean Woods; occurring in every compartment. It should be noted also that *Carychium tridentatum*, which is also supposed to prefer moderately moist conditions, was the most abundant species. Although specifically searched for, no *C. minimum* were found.

In view of the difficulty in establishing whether a woodland is 'Primary' (never been cleared) rather than 'Ancient' (continuous cover since 1600 AD) and the evidence that West Dean Woods Nature Reserve may be 'Ancient' rather than 'Primary' there may be a case for modifying the indication value of certain species. Thus, *Acicula fusca* could be a useful indicator of 'Ancient' woodland (as already interpreted by Wardhaugh, 1997) rather than 'Primary' (Kerney & Stubbs, 1980) without in any way detracting from either its interest or the value of the woodland it is present in. Similarly, the presence of *Limax tenellus* and *Limax cinereoniger* (the latter also in the adjacent 20 year old pine plantation, planted into cleared and burnt derelict coppice, later weeded, herbicided and brushed, unpublished data) at West Dean, suggests that either they are tolerant of some disturbance, or else able to recolonise disturbed areas. Bishop (1976) noted that *L. cinereoniger* was common in plantations in Somerset.

Because West Dean Woods Nature Reserve has been coppiced, probably extensively, in the past, any mollusc species which have been unable to accommodate the disturbance caused by coppicing are likely to have become extinct a long time ago. The species found have demonstrated their ability to adapt and survive under coppice management. As the area is now surrounded by plantation and pasture it is unlikely that a reservoir for disturbance intolerant species remains nearby. Our results show it is possible to separate snail species in terms of litter, vegetation and pH, but less easy to separate in terms of compartment age.

ACKNOWLEDGEMENTS

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SYSTEMATICS, DISTRIBUTION AND HYBRIDIZATION OF *MELANOPSIS* FROM THE JORDAN VALLEY (GASTROPODA: PROSOBRANCHIA)

J. HELLER[1], N. SIVAN[1] & U. MOTRO[1]

Abstract   Melanopsis *is a highly variable freshwater genus. We describe its systematics, distribution and extent of hybridization in the Jordan Valley. Our study is based upon conchiometrics of 760 snails, from 38 sites.*

Three species are recognized: Snails with smooth shells (M. buccinoidea*); with straight-ribbed shells in which the ribs extend almost the entire height of the ultimate whorl (*costata*); and with tubercle-ribbed shells in which the ribs usually extend about half the height of the ultimate whorl (*saulcyi*). Hybrids are found in zones of sympatry, both between* buccinoidea *and* costata *and between* buccinoidea *and* saulcyi*, at low frequencies and over distances of no more than a few hundred m.*

Within costata *we distinguish three groups, and tentatively suggest that they may be subspecies. Shells from the upper Jordan River are elongate (c. costata); those from Lake Kinneret are stout (c. jordanica); and in those of the Yarmouk each rib consists of a pronounced upper tubercule, fused to a pronounced, straight lower ridge (c. noetlingi). Within* buccinoidea*, shells from Nahal Dan differ in their shallow notch and small mouth-height.*

The small, stout shell of c. jordanica *correlates with a stormy habitat. A stout, globose shell could accommodate more foot muscle and thus enable a stronger adherence to rocks and boulders during severe storms.*

Key words   Melanopsis, *systematics, distribution, hybrids, variation, Jordan Valley*

INTRODUCTION

The freshwater snail *Melanopsis* (Melanopsidae) has a broadly circum-mediterranean distribution (Germain, 1921–2; Banarescu, 1990–95) and its many isolated populations exhibit widely divergent shell phenotypes. Its anatomy has been described by Bilgin (1973), sperm structure by Afzelius, Dallai & Callani (1989), radula variation by Glaubrecht (1993) and allozyme variation (in the western Mediterranean) by Altaba (1991), who found considerable genetic differentiation over short distances.

In the Levant the first reference to *Melanopsis* is by Olivier (1801, 1804) concerning *buccinoidea* and *costata*. Over the eighty years that followed Olivier, major contributions were by Roth (1839, who described *M. costata* var. *jordanica*), Bourguignat (1853, who described *saulcyi*), Tristram (1865, *ammonis, eremita*) and Locard (1883, *chantrei, lortetiana*). In 1884 Bourguignat wrote a massive monograph in which he described 93 *Melanopsis* species, including many new ones. Many of these new descriptions were based upon de Saulcy's collection, which has since been lost. As Bourguignat did not illustrate his many new species and as his types are today unavailable, his monograph is today regarded as an obstacle rather than a contribution to *Melanopsis* taxonomy (Schütt & Bilgin, 1974). From the land of Israel alone he listed 27 species.

In the years that followed Bourguignat's monograph there were several attempts to put some order into the taxonomy of *Melanopsis* of the Levant. Dautzenberg (1894) who studied material collected by Barrois, reduced this list to seven; and Germain (1921–2), who studied molluscs from Syria collected by de Kerville, further reduced this list to six. Pallary (1939) collected in Syria and Lebanon but concerning Israel he relied mainly upon specimens collected by J. Petrbok, which he assigned to *buccinoidea, prophetarum,*

[1] Department of Evolution, Systematics and Ecology, The Hebrew University of Jerusalem, 91904 Jerusalem, Israel

desertorum, and *cerithiopsis.* Pallary was a splitter, and from the entire Levant (Syria, Lebanon, Israel and Jordan of today) he described 18 species.

Tchernov (1975a) collected mainly in and near Lake Kinneret. He concluded that in *Melanopsis* there are vast numbers of ecotypes, all belonging to a single circum-mediterranean species that he named *M. praemorsum.* Tchernov (1973, 1975a) suggested that costated shells are found in large open water bodies, where the ribs protect the animal against storms; smooth shells inhabit small streams, rivers and springs; and weakly-developed costae are found where high temperatures coincide with high salinity. Bilgin (1973) however found that *praemorsa* and *costata* are different species, as based on the shell shape and radula. Mienis (1983) at first suggested three species, *M. praemorsa, M. costata* and *M. cerithiopsis,* the latter confined to the lower Jordan Valley. Ten years later Mienis & Ortal (1994) presented a different classification, that included *M. praemorsa buccinoidea, M. p. eremita, M. p. jordanica, M. saulcyi* and *M. cerithiopsis.* Schütt (1965, 1987, 1988a–b; Schütt & Sesen, 1989) assigned all *Melanopsis* of the Levant to *M. praemorsa.* From Syria he described *p. ferussaci, p. costata, p. olivieri, p. obsoleta* and *p. nodosa;* from Jordan *p. bandeli.* Burch (1985) and Burch, Bruce & Amr (1989) assigned the *Melanopsis* of Jordan to two subspecies, *praemorsa buccinoidea* and *p. costata.* Raanan (1986) found that the black and banded morphs of *costata* in Lake Kinneret differ in their conchiometrics and micro-distribution, and suggested that they belong to two separate species, with incomplete reproductive isolation. Marko (1984) and Altman & Ritte (1996) however could not find electrophoretic differences between these two morphs. Glaubrecht (1993, 1996) analysed specimens from the entire circum-Mediterranean range of *Melanopsis,* including material collected by Bandel in Jordan. He suggested only a single, highly polymorphic circum-Mediterranean superspecies, *Melanopsis praemorsa,* the subspecies of which display minor anatomical variation in radula but dramatic differences in shell sculpture. In the Levant he recognized two subspecies, *buccinoidea,* and *costata,* that widely hybridize to such an extent that they are conspecific (Glaubrecht 1993; 1996: 265).

Taxonomic analysis may get out of hand when shell variation of a very large geographic region, such as the entire Levant, is considered simultaneously. A more cautious approach may be to start by collecting snails from many sites within one small region, analysing their conchiometrics and developing a taxonomy that concerns only that small region; and only later to extend research, both into further regions and into other (e.g. molecular) characters. One small region of exceptional interest for evolutionary studies is the Jordan Valley. It contains numerous fossil strata rich in *Melanopsis* remains, some of which date 2–3 million years BP; these have been subject to several detailed analyses (Picard, 1934; Tchernov, 1973, 1975b; Moshkovitz & Magaritz, 1987; Schütt & Ortal, 1993 and references therein). A detailed analysis of recent *Melanopsis* of the Jordan Valley may provide a basis for future comparisons with these fossils.

The aim of this paper is to describe, through shell morphometry, the systematics, distribution and extent of hybridization of recent *Melanopsis* in the Jordan Valley.

METHODS

SAMPLING

This study is based mainly upon the measurements and analysis of 740 shells collected at 37 sites, all within an area of approximately 100 x 25 km (Figs 6 and 7; site names follow the English version of the 1:250,000 map of the Survey of Israel, 1987); and of another 20 snails collected from the lower Jordan near its outlet into the Dead Sea, 60 km further south of the main area of study (south of the Allenby Bridge). At each site
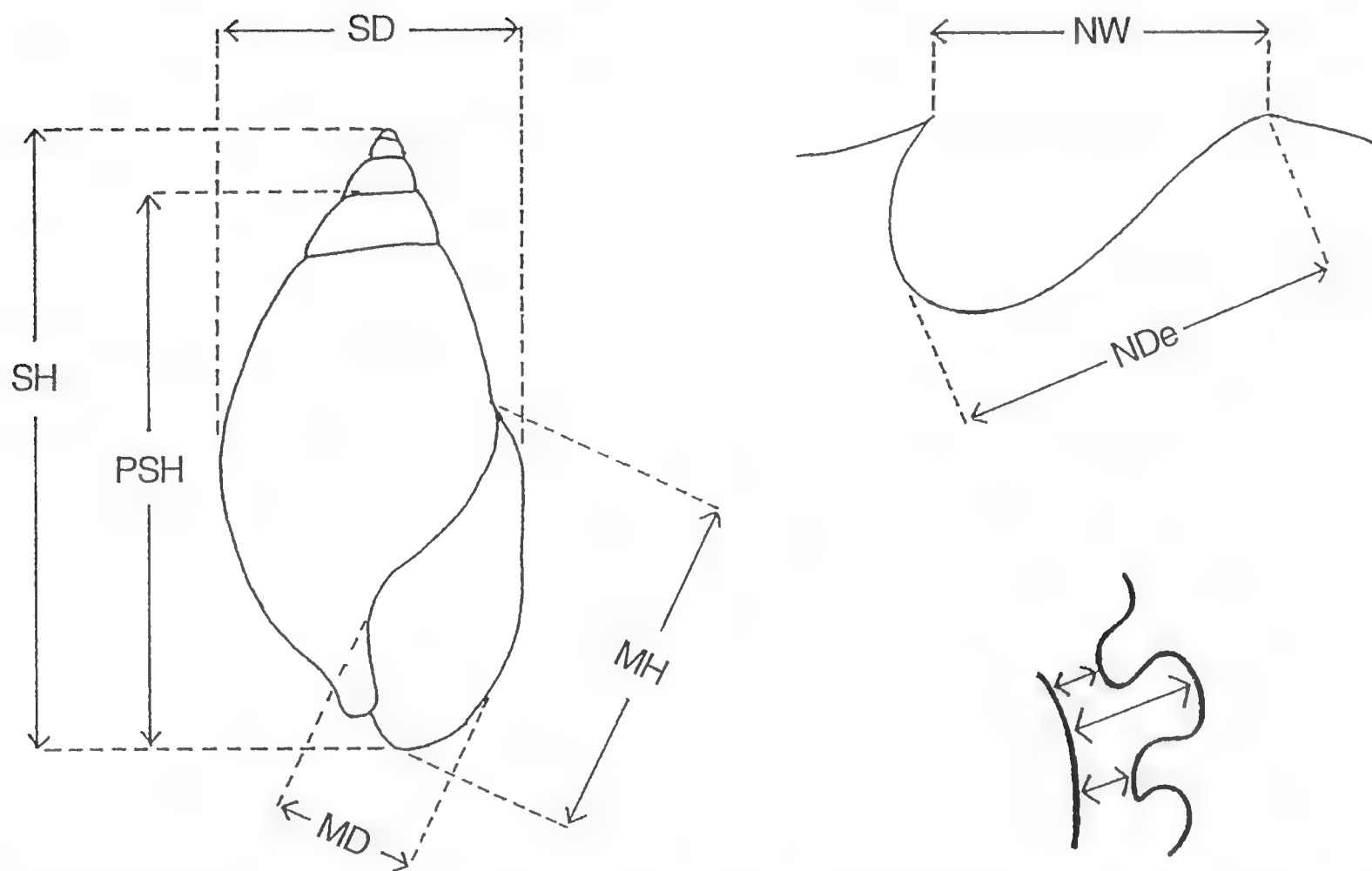
Fig. 1 Measurements used in this study. Left: Shell (viewed from front). Upper right: Notch (viewed from below). Lower right: Rib height (shell thickness at rib center, minus average shell thickness at rib sides in a transected shell). SD - shell diameter; SH - shell height; PSH - partial shell height; MD - mouth diameter (the widest diameter at a right angle to mouth height); MH - mouth height; NDe - notch depth; NW - notch width.

we collected 20 snails, within an area of no more than 10 m². Where both clearly smooth and costated shells were present at the same site, we collected 20 of each type.

The *Melanopsis* collected for this research are kept in the National Mollusc Collection of the Hebrew University, Jerusalem.

MEASUREMENTS AND RATIOS

Conchiometrics (Fig. 1) include shell height (SH), shell diameter (SD), mouth height (MH) and mouth diameter (MD) (measured with an image analyser); notch width (NW) and notch depth (NDe) (measured under binocular, using an eye-piece micrometer). All measurements are in millimeters, accurate to 0.1 mm.

From these measurements, seven ratios were calculated:

shell-diameter / shell-height
mouth-height / shell-height
mouth-diameter / mouth-height
mouth-height / shell-diameter
notch-width / notch-depth
notch-width / mouth-diameter
notch-depth / mouth-diameter.

(Relationships between measurements are isometric; therefore problematics concerning allometric variation, as mentioned by Atchley, Gaskins & Anderson (1976) and Atchley & Anderson (1978), are not relevant to this study).

In addition to measurements and ratios, each shell was also scored for presence or absence of ribs. Where ribs were present, on each shell three rib characteristics were scored:

• Number of ribs, from point of insertion of the aperture on the body whorl right-wards, to the corresponding point on the penultimate whorl.

• Rib length, examined on body whorl. This characteristic is continuous. To describe

increasing rib length four categories were erected, and numbered 1–4:
    1. ribs very short, do not reach the shell aperture.
    2. ribs reach from the suture down to the aperture.
    3. ribs reach beyond the aperture but do not extend the entire height of the body whorl; usually they reach midway down the aperture.
    4. ribs reach the entire height of the body whorl.
• Rib shape, examined on body whorl. Also this characteristic is continuous. To describe increasing levels of 'bumpiness' four categories were erected, and numbered 1–4:
    1. Each rib consists of an upper tubercle, near the suture; and an elongate ridge beneath it. The ridge is continuous with the tubercle and there is no depression between them. There is a gradual decrease in overall rib width, from upper to lower end of each rib.
    2. There is no tubercle and rib width is uniform (not decreasing from upper to lower end of each rib).
    3. Each rib consists of an upper tubercle, near the suture; and an elongated ridge beneath it. There is a slight depression between the tubercle and ridge.
    4. Each rib has an upper tubercle, near the suture; beneath it there is a second tubercle. The two tubercles are separated by a considerable depression.

A ratio that combines shell conchiometry and rib number was also calculated. This is the Rib index, defined as the ratio

$$\frac{\text{Shell-diameter/Shell-height}}{\text{number of ribs}}$$

In seventy shells from various sites also rib height was measured: each shell was first cut with a delicate disc-saw to obtain a cross-section and then abraded, with an electric grind-stone, down to a standard level (through the lower whorl, at the uppermost corner of the shell aperture ± 1 mm). In this cross-section, shell thickness was measured (with a micrometer) at the center and on both sides of the most prominent rib. Rib height was defined as shell thickness at rib center, minus shell thickness at (averaged) rib side.

In most sites we were careful to measure only uneroded shells, but in all samples from Lake Kinneret most snails were eroded. In these eroded shells of Lake Kinneret we calculated shell height as follows: in each sample, in five uneroded shells we measured both the standard shell-height; and also 'partial shell height', determined as the distance from the lower part of the aperture to a point on the penultimate suture above the base of the columella (Fig. 1). In the eroded shells, to estimate shell height we first measured partial shell height; and then multiplied this measurement by the ratio shell-height / partial-shell-height, obtained from the uneroded shells.

Intermediates between ribbed and smooth shells were found at some sites. In these sites several samples, of 50 snails each, were collected over short distances (which we describe in the text). In the lab all these snails were examined carefully under a binocular and scored as ribbed, smooth or intermediate; they were not measured.

For future comparisons with the highly variable recent and fossil shells of *Melanopsis*, measurements and ratios of each separate sample are given (in Appendix 1) in addition to the overall values of each species.

Statistics

For the statistical analysis we entered all ratios, presence-absence of ribs, and most rib characteristics. Additional characters recorded but not entered into the statistical analysis concern details of the upper tubercle of each rib. Also, we did not enter colour:

TABLE 1

Comparisons of shell characteristics of *M. buccinoidea* (M. b.), *M. c. costata* (M.c.c.), *M. c. jordanica* (M.c.j.) and *M. saulcyi* (M.s.). ** denotes P<0.01, * denotes 0.01<P<0.05, NS denotes a non-significant difference. P values were not subject to Bonferroni adjustment.

	M.b./M.c.c.	M.b./M.c.j.	M.b./M.s.	M.c.c./M.c.j.	M.c.c./M.s.	M.c.j./M.s.
Shell diameter/shell height	**	**	**	**	*	**
Mouth diameter/mouth height	**	**	**	*	NS	NS
Notch width/notch depth	NS	NS	**	NS	**	**
Notch depth/mouth diameter	**	**	NS	NS	**	*
Number of ribs	-	-	-	NS	**	**
Rib length	-	-	-	*	**	**
Mouth height/shell height	**	**	**	NS	**	**
Mouth height/shell diameter	**	**	**	**	NS	**
Notch width/mouth diameter	**	**	*	NS	**	**
Rib form	-	-	-	NS	**	**
Rib index	-	-	-	**	**	**

overall colour of the shell, presence-absence of bands, number of bands, colour of bands, and relative width of dark and light bands. Colour terminology follows Kornerup & Wanscher (1984).

The clustering analysis, represented in the dendrograms of Figs 2 and 3, was performed in the following way. First, we calculated the standardized Euclidean distance between any two individuals (see, for example, Abbott, Bisby & Rogers, 1985). Next, the distance between any two locations (A and B, say) was defined as the unweighted average of the distances (calculated in the previous stage) over all relevant pairs, that is, pairs in which one individual belongs to location A and the other to location B. The between-location distances thus obtained were used to construct the dendrograms in Figs 2 and 3, using the unweighted pair group average method.

Since the various characters considered are perceivably inter-correlated, our suggested method of calculating the between-location distance as the mean of between-pair distances, has an obvious advantage over the commonly used method of calculating the between-location distance as the distance between the vectors of the location
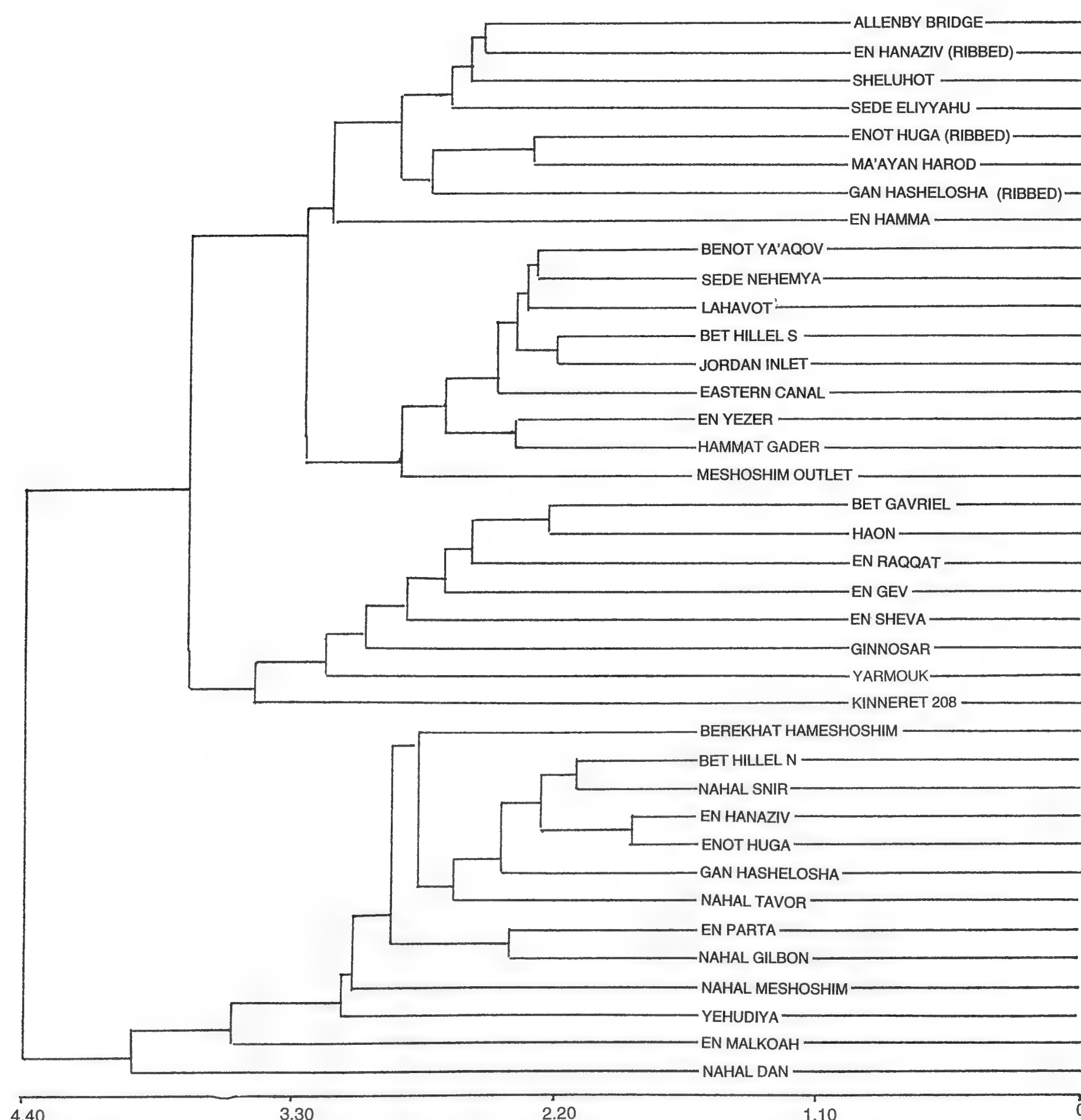
Fig. 2   Dendrogram based upon shell proportions, notch proportions and presence / absence of ribs; all 38 samples.

means.

For each of the taxonomic groups we present the means (with standard errors) of the various characters, taking into consideration that sampling was done in two stages: locations from each taxonomic group, and individual snails from each location.

For each character, the means were compared between any two taxonomic groups using two-level nested ANOVA.

CLUSTER ANALYSIS

Two different dendrograms (Figs 2, 3), based upon conchiometric similarity, present relationships among the 38 samples of this study.

The first dendrogram (Fig. 2) is based upon the seven shell and notch proportions (see methods), and also upon presence versus absence of ribs. All thirteen samples of non-ribbed shells fall into one group, with Nahal Dan as the most extreme. The twenty-five

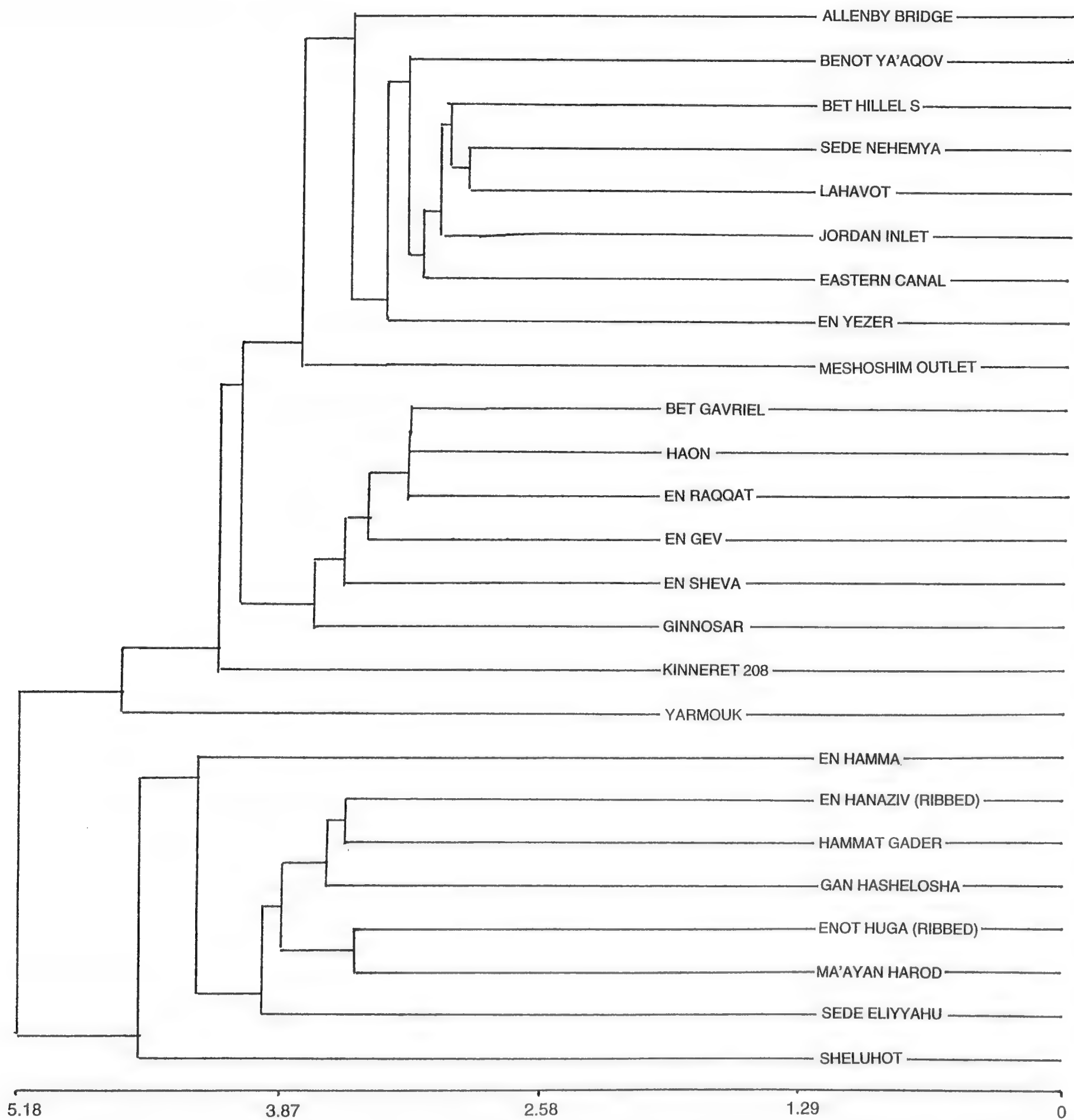**Fig. 3** Dendrogram based upon shell proportions, notch proportions and all rib characters; 25 samples containing only ribbed shells.

samples of ribbed shells fall into another group, which is sub-divided into three sub-groups.

The second dendrogram contains only those twenty-five samples with ribbed shells. It adds the four rib characters to those used in Fig. 2, and thus gives (for the samples with ribbed shells) a clustering that is based upon more characters. We can see (Fig. 3) that the first group of ribbed shells contains the seven samples north of Lake Kinneret (upper Jordan River), and one (Allenby Bridge) from the lower Jordan River. The Meshoshim Outlet sample also falls in or near this group. The second group of ribbed shells contains seven samples from Lake Kinneret, with Kinneret 208 as the most extreme. The Yarmouk sample falls close to this group. The third group of ribbed shells contains the eight samples from the Bet Shean - Hammat Gader area. The first two groups fall close together; the third group is more separate.

The differences between Fig. 2 and Fig. 3 are small: even without the rib-characters most of the ribbed samples fall into their final position already in the first dendrogram.

We use these dendrograms as our basis for classifying the 38 samples. Table 1 presents statistical comparisons (two-level nested ANOVA) between the four main taxa which will now be described: *Melanopsis buccinoidea*, *M. costata costata*, *M. c. jordanica* and *M. saulcyi*. Concerning the Yarmouk sample, we diverge from the dendrograms. We consider this sample as a separate taxon, *M. c. noetlingi*, on the ground of rib height, which was measured only upon few shells (see Methods).

SYSTEMATIC DESCRIPTION

MELANOPSIDAE
Genus *Melanopsis* Férussac
Type species: *Melanopsis praemorsa* (L.) from southern Spain.

Definition   The shell is thick and solid, imperforate, and may be smooth or heavily ribbed. A distinctive notch is present at the base of the mouth, where the outer and inner lips meet. The upper part of the shell aperture is very narrowly constricted and the inner lip usually contains a callus. In the lower half of the inner lip, the columella is truncate.

Melanopsis buccinoidea Olivier 1801
Fig. 4A

M. buccinoidea (Olivier 1801, pl. 17 Fig. 8).
Melanopsis buccinoidea Pallary,1939 pl. 6 Figs 1–4, 64–65.
Melanopsis prophetarum Pallary 1939, pl. 6 Figs 16–17, 36, 57.
Melanopsis desertorum Bourguignat, 1884.
Melanopsis desertorum Pallary 1939, pl. 6 Figs 58–59.
Melanopsis praemorsa L., Tchernov 1975, Figs 21–22.
Melanopsis buccinoidea L., Glaubrecht 1993.

Holotype and Type locality   "Melanie buccinoide, *M. buccinoidea* de Scio". (Olivier 1801, pl. 17 Fig. 8).

Material examined   Nahal Dan, Nahal Senir, Bet Hillel North, Nahal Gilbon, Berekhat HaMeshoshim, Yehudiya, Nahal Meshoshim, Nahal Tavor, Enot Huga, Gan Hashelosha, En Hanaziv, En Parta.
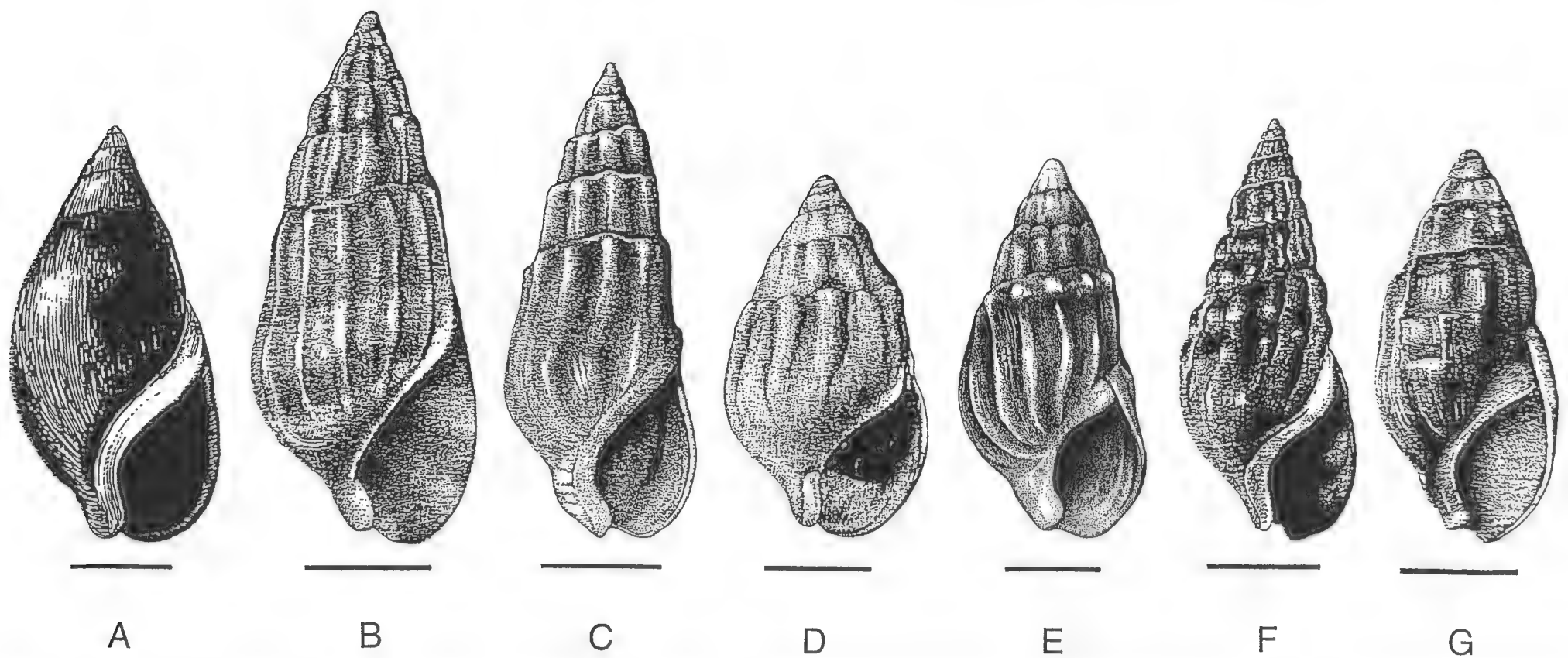
Fig. 4   *Melanopsis* taxa of the Jordan Valley. **A** *M. buccinoidea* (Nahal Senir); **B** *M. costata costata* (type, Lahavot); **C** *M. costata* ssp. (Allenby Bridge); **D** *M. costata jordanica* (En Gev); **E** *M. costata noetlingi* (Yarmouk); **F** *M. saulcyi* (En HaNaziv); **G** *M. saulcyi* (Enot Huga). Scale bar = 5 mm.

Measurements

Shell Character	Range	Mean ± S.E.
shell-height	up to 26.0 mm	
shell-diameter	up to 13.5 mm	
mouth-height	up to 16.1 mm	
mouth-diameter	up to 6.3 mm	
notch-width	up to 3.1 mm	
notch-depth	up to 3.5 mm	
shell-diam / shell-height	0.45–0.56	0.498 ± 0.003
mouth-height / shell-height	0.48–0.68	0.596 ± 0.007
mouth-diameter / mouth-height	0.33–0.48	0.399 ±0.005
mouth-height / shell-diameter	0.97–1.36	1.197 ± 0.012
notch-width / notch-depth	0.60–1.33	0.922 ± 0.021
notch-width / mouth-diameter	0.30–0.68	0.465 ± 0.012
notch-depth / mouth-diameter	0.29–0.75	0.507 ± 0.003

(Overall measurements. Detailed measurements of the different samples are in Appendix 1A.)

Description   The shell has up to seven whorls. It has a pointed spire, flattened whorls separated by very shallow sutures, and is smooth. Shell colour is almost always uniform black, or reddish brown; when not completely black, the upper half of the shell is darker than the lower half. On some shells the colour is not uniform. Rather, each ultimate whorl has three dark spiral bands (black or dark brown) between two pale ones (reddish brown or greyish yellow), and the upper whorls have one dark and one pale band. Also, in some shells the white callus of the upper parietal wall merges with the white columella.

The Nahal Dan sample differs from other samples in its more shallow notch (Fig. 5A; see also Appendix 1A, ratios notch-width / notch-depth). It differs also in its small aperture height, relative to shell-height (Fig. 5B; see also Appendix 1A). Further variation within *buccinoidea* concerns shell colour. In ten samples all shells were uniformly coloured, reddish brown-to-black (Nahal Dan, Nahal Senir, Bet Hillel, Nahal Gilbon,

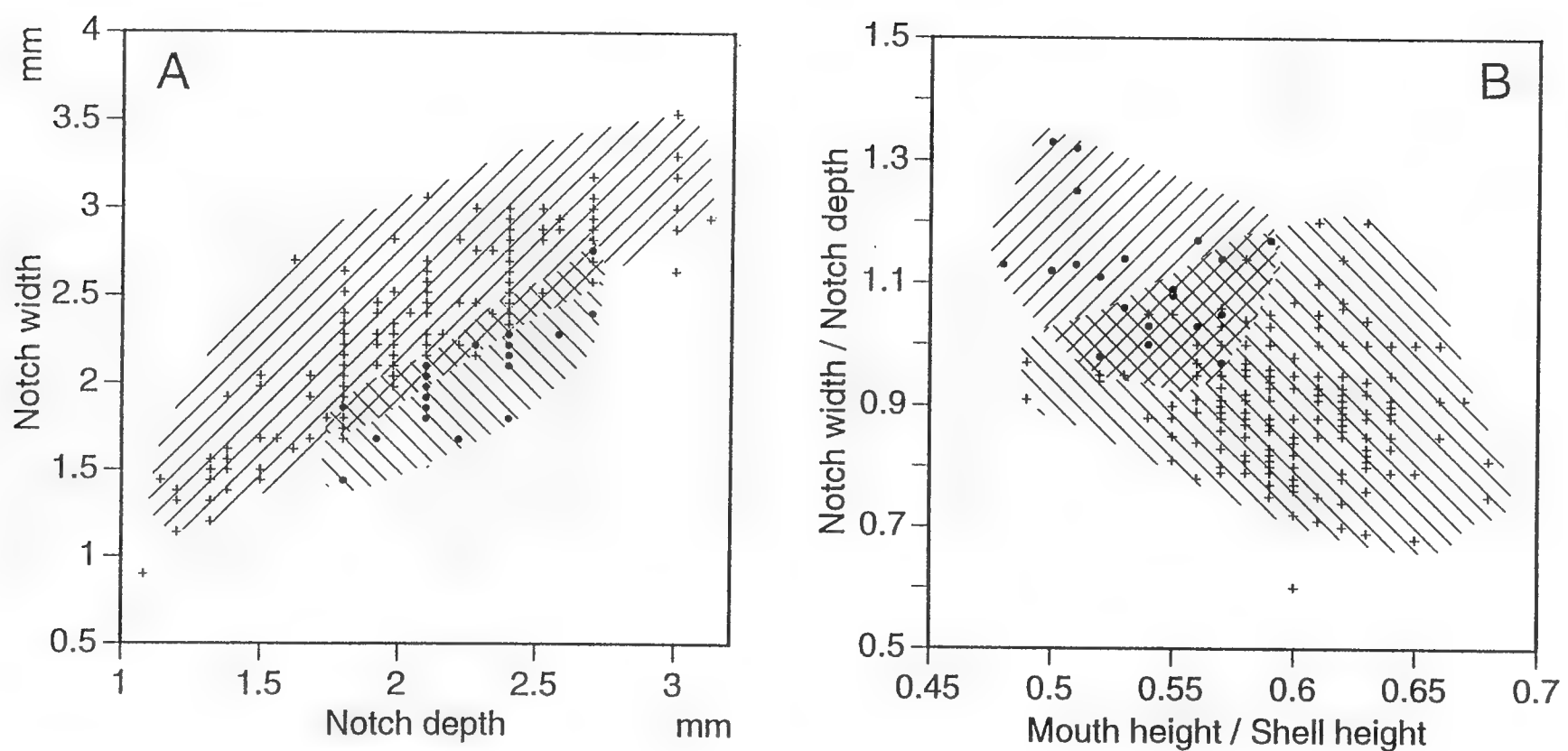**Fig. 5**   The Nahal Dan sample (●) as compared to all other *M. buccinoidea* samples (+). **A** The ratio notch-width versus notch-depth. **B** The ratio notch-width / notch-depth versus the ratio mouth-height / shell-height.

Nahal Tavor, Enot Huga, Gan HaShelosha, En HaNaziv and En Parta). In three samples, all along Nahal Meshoshim, some shells had spiral bands (in the Nahal Meshoshim sample 37% of the shells were banded, the paler bands being so dark brown that they were hard to distinguish; in Gesher Yehudiya 42% and in Berekhat HaMeshushim 37% of the snails were banded, and there was considerable variation in the colour of both the dark and the pale bands). Altogether 9% of the shells in our samples were banded.

Habitat   A wide variety of aquatic habitats, from small trickles to springs and streams. Usually it occupies stones (basalt or limestone), sometimes also silty mud.

Geographic range   Throughout the Jordan Valley, from the tributaries of the Jordan River (Hatsbani, Banias and Dan) down to Jericho; absent from the Jordan River and Lake Kinneret.

Remarks   Buccinoidea is the oldest name of a smooth-shelled *Melanopsis* from the Levant. We could not discern differences between our shells and the figure given by Olivier, or the cotypes of *buccinoidea* illustrated by Pallary (1939, pl. 6 Figs 1–4, 64–65) from Sin el Fil (Syria) and from Beirut (Lebanon). The type species of *Melanopsis*, *M. praemorsa* L, occurs in Spain; it too is smooth shelled but is described as differing from *buccinoidea* in its smaller, more ventricose shell (Pallary, 1939). Whether *M. buccinoidea* is a species completely separate from *praemorsa* (as suggested by Pallary, 1939), a subspecies within a big *praemorsa* superspecies (as suggested by Schütt, 1983 and Glaubrecht, 1993), or merely a synonym of *praemorsa* (as suggested by Tchernov, 1975a) is beyond the scope of this present study. Bourguignat (1884) described *M. prophetarum* (from the the environs of Jericho, Banias, Jenin and Lake Hula) as differing from *buccinoidea* in that the upper part of the last whorl is subangular; and Pallary (1939) redescribed and illustrated *M. prophetarum* Bourguignat 1884 from 'Sachne beit Alfa' (today the Gan Hashelosha) and Jericho (Pl. 6, Figs 16–17, 36, 57). We find this (slight) character so variable within samples, and his figures so similar to our shells, that we consider *prophetarum* a synonym of *buccinoidea*. Bourguignat (1884: 134–5) described *Melanopsis desertorum* from Ain el Bass (in the Hula swamp) and this was mentioned and illustrated by Pallary (1939). Pallary's illustration of this species (pl. 6 Figs 58–59) is similar to *buccinoidea*, whereby

we consider it a synonym. Tchernov's illustrations (1975a, Figs 21–22) of *M. praemorsa* from the Tabgha spring near Kinneret represent typical *buccinoidea*.

Melanopsis costata Olivier 1804
Figs 4B, 4C, 4D, 4E.

Melania costata (Olivier 1804, pl. 31 Fig. 3.)
Melanopsis costata Olivier in Pallary 1939, Fig. 12.

Holotype and Type locality   "Menalie a cotes, Melania costata; de Orontes" (Olivier 1804, pl. 31 Fig. 3.)

Material examined   Bet Hillel South, Sede Nehemya, Lahavot, Eastern Canal, Benot Ya'aqov, En Yezer, Jordan Inlet, En Sheva, Ginnosar, En Raqqat, En Gev, Haon, Bet Gavriel, Meshoshim Outlet, Kinneret 208, Yamouk, Allenby Bridge.

Measurements   Will be presented separately for each subspecies (see below).

Description   The 2–4 upper whorls are smooth, the 3–6 lower whorls are ribbed. Ribs extend the entire height of each whorl and most of them descend vertically; usually however, two–four ribs above the shell aperture bend leftwards, towards the base of the columella. In some shells only the lower part of these ribs bend, in others the entire rib tends in a leftward, diagonal direction. The upper section of each rib (near the suture) is almost always rounded.

   Shell colour varies from greyish yellow to black; reddish brown is also found, but not common. The colour is usually uniform, with no clear border between the upper and lower part of the shell. Some shells are banded. The white callus of the upper parietal wall merges with the white columella, so the entire inner lip is white.

Geographic range   Upper Jordan River, Lake Kinneret and lower Jordan River. *M. costata* is broadly parapatric with *buccinoidea*.

Comparisions   *M. costata* differs from *M. buccinoidea* in its ribbed shell.

Remarks   Of the nine sites along the Jordan River where *costata* was found, in seven no *buccinoidea* was found; in Bet Hillel (IG 207290, not included in statistics) merely 4% of the snails were *M. buccinoidea*, and in Bet Hillel south (IG 207289) 25%. (1 km further north, in Bet Hillel north, there were only *buccinoidea*).

   To examine hybridization between *costata* and *buccinoidea*, three transects were made along three streams that flow into the Kinneret: In Biq'at Bet Zaida Nature Reserve we sampled and mapped in detail, along Nahal Meshushim (mainly) and into Lake Kinneret. Altogether 19 samples were collected, from within an area of 2x2 km. The samples, each of 50 snails, were a few hundred m apart, and each was collected from an area of 10 m². In En Sheva (Tabgha in earlier maps) the transect (from lake Kinneret shoreline to the walls of the German Hospice) was 90 m long and along it, at each 10 m interval, 50 snails were collected from a strip 1 m wide. At En Ra (Fulliya in earlier maps); the transect (from lake shoreline to the spring) was 40 m long and also here at each 10 m interval 50 snails were collected, from a strip 1 m wide. The Biq'at Bet Zaida transect was collected in August 1996, the other two in January 1997 (when the water level of Lake Kinneret was very low, –211.60 m). In the lab each shell was classified as *costata*, *buccinoidea* or hybrid. Hybrid was defined as a shell in which costae occur, but are weakly developed; or as a shell in which no ribs occur, but the sutures are deep. To

90 m

10 km

N. Senir

N. Dan

Bet Hillel

Sede Nehemya

Lahavot

Eastern Canal

N. Gilbon

Benot Ya'aqov

JORDAN R

Berekhat
HaMeshushim

N. Meshushim

En Yezer

Yehudiya

-208

En Sheva

Ginnosar

LAKE
KINNERET

En Raqqat

En Gev

0 m

30 m

0 m

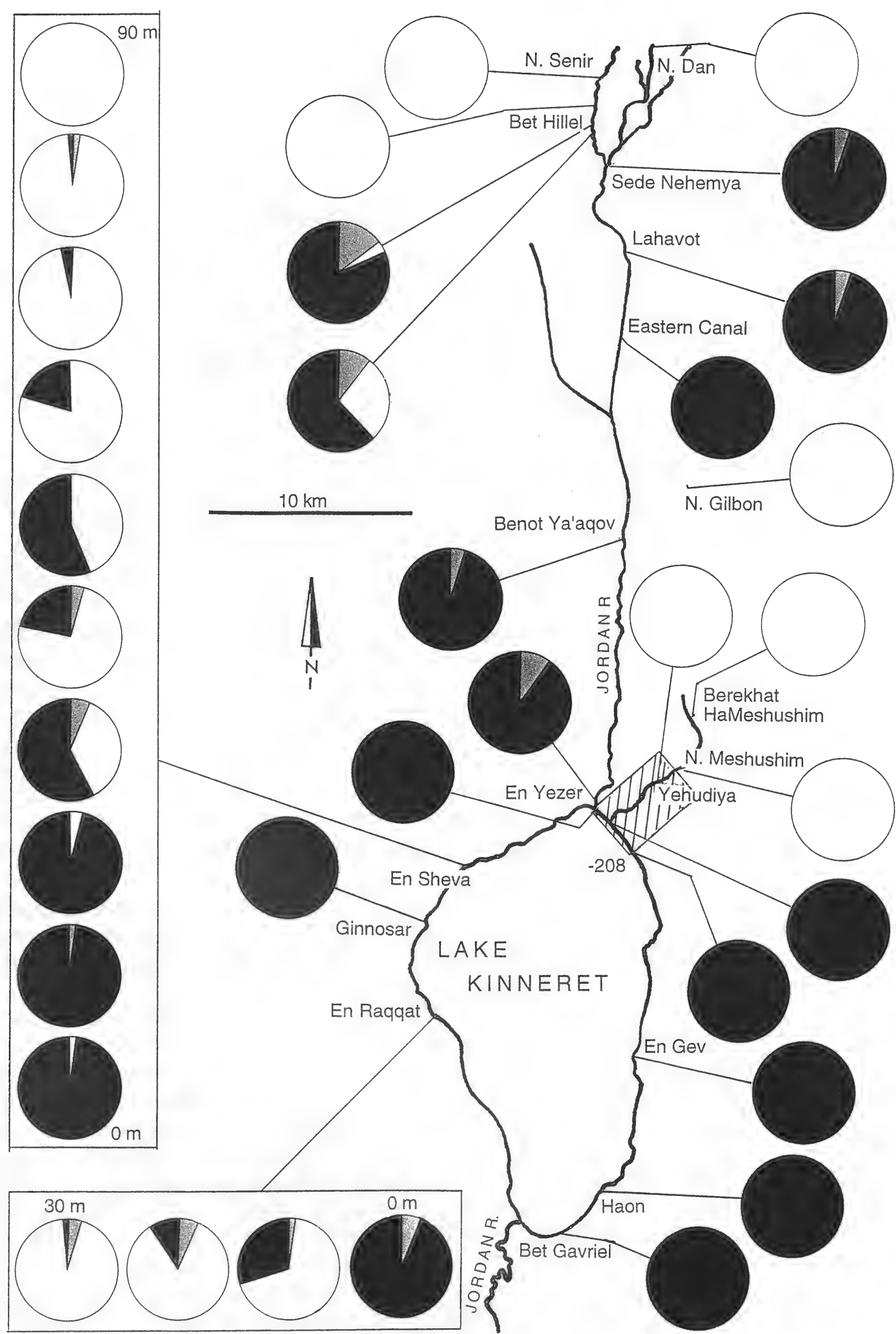Haon

JORDAN R.

Bet Gavriel

JORDAN R.

Fig. 6 Frequency of *M. buccinoidea* (white), *M. costata* (black) and hybrids (gray), in samples of the upper Jordan River and Lake Kinneret. All costata of Lake Kinneret are *c. jordanica*, elsewhere - *c. costata*.Left rectangle: Frequencies in a 100 m transect, from the shores of Lake Kinneret (bottom) up along one of the En Sheva springs that flows into the lake. In each sample n = 50. Low rectangle: Frequencies in a 40 m transect, from the shores of Lake Kinneret (right) up along one of the En Raqqat springs that flows into the lake. In each sample n = 50. The hatched rectangle on the north-east of Lake Kinneret is enlarged in Fig. 7.

be confident of our results each sample was classified twice; differences were negligible.

Along the En Sheva and En Raqqat transects most shells could be classified into either *M. costata* or *M. buccinoidea*, which coexist as distinct forms (Fig. 6). From lake to spring there is a smooth, monotonic decrease of *costata* and a corresponding increase of *buccinoidea*. Hybrids do occur, but at low frequencies of 2–6% of each sample. Also along the Biq'at Bet Zaida transect most shells could be classified into either *costata* or *buccinoidea*, which may coexist as distinct forms (Fig. 7). Hybrids occurred 1.3 km along the stream but (in Nahal Meshoshim) the four samples in which they formed 25% or more were all within a short distance of 300 m; in Nahal Dalyyot, 800 m to the south, another sample with high frequencies of hybrids was found. To conclude most hybrids at Biq'at Bet Zaida were confined to a narrow zone of a few hundred meters. Beyond these transects we did not find any *buccinoidea* or hybrids in any of the Kinneret samples.

Hybrids between *M. buccinoidea* and *M. costata* were also found in most Hula sites, at a low frequency (Fig. 6). Of the shells collected at seven Hula sites, 5.0% were hybrids in that they were weakly ribbed or deeply sutured.

Within *costata* we distinguish three groups, that differ significantly (not diagnostically) in their conchiometrics and distribution. We suggest that these groups may be subspecies and we have tentatively assigned them the names *c. costata, c. jordanica* Roth and *c. noetlingi* Bourguignat.

<center>

Melanopsis c. costata
Figs 4B.

</center>

Melania costata (Olivier 1804, pl. 31 Fig. 3.)
Melanopsis cerithiopsis Pallary 1939 pl. 4 Fig. 10.
Melanopsis germaini Pallary 1939 pl. 6 Fig. 8.
Melanopsis saulcyi Pallary 1939 pl. 6 Fig. 27 and pl. 6 Fig. 29.

Holotype and Type locality "Menalie a cotes, Melania costata; de Orontes" (Olivier 1804, pl. 31 Fig. 3.)

Material examined Bet Hillel South, Sede Nehemya, Lahavot, Eastern Canal, Benot Ya'aqov, En Yezer, Jordan Inlet, Meshoshim Outlet, Allenby Bridge.

Measurements

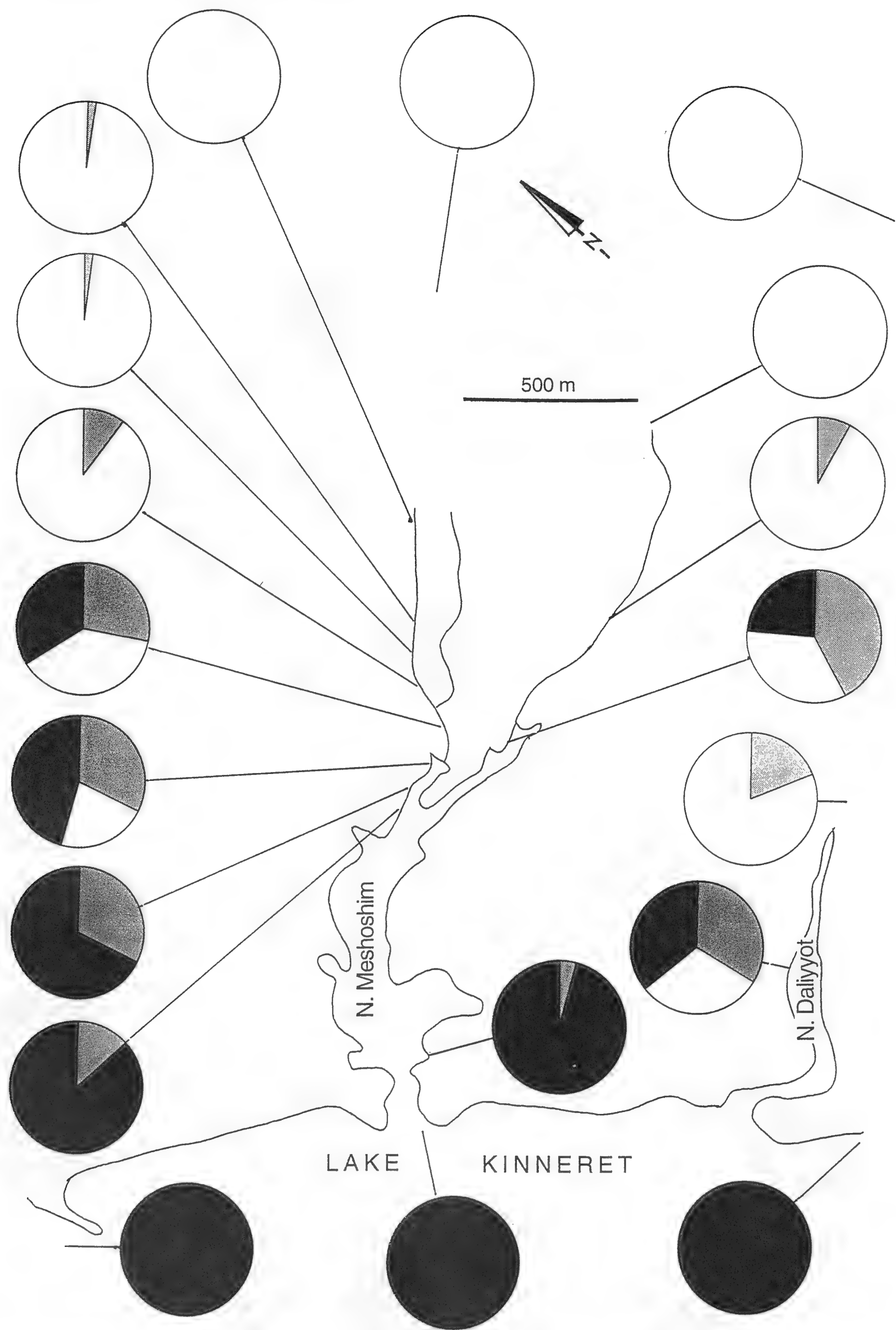| Shell Character	Range	Mean ±S.E.
shell-height	up to 29.2 mm	
shell-diameter	up to 13.2 mm	
mouth-height	up to 15.3 mm	
mouth-diameter	up to 6.8 mm	
notch-width	up to 3.9 mm	
notch-depth	up to 3.9 mm	
shell-diameter / shell-height	0.39–0.56	0.475 ±0.003

Fig. 7 Frequency of *M. buccinoidea* (white), *M. costata* (black) and hybrids (grey) shells in a transect, from the shores of Lake Kinneret into Biq'at Bet Zaida. In each sample n = 50.

mouth-height / shell-height	0.44–0.63	0.541 ± 0.006
mouth-diameter / mouth-height	0.38–0.52	0.435 ± 0.003
mouth-height / shell-diameter	1.01–1.30	1.144 ±0.008
notch-width / notch-depth	0.76–1.11	0.911 ± 0.013
notch-width / mouth-diameter	0.39–0.76	0.524 ± 0.002
notch-depth / mouth-diameter	0.40–0.76	0.577 ± 0.002
number of ribs	9–14	11.086 ±0.151
rib form	1–3	1.771 ± 0.063
rib length	3–4	3.546 ± 0.040
rib index	3.3–5.6	4.333 ± 0.058

(Overall measurements of *c. costata*. Detailed measurements of the different samples are in Appendix 1B).

Description   The shell is tall and elongate; the ribs are mildy pronounced, and their shoulders are rounded.

Shell colour varies, but generally the reddish brown-to-black colour is far less common than in *M. buccinoidea*. In Gesher Hayarden all shells were greyish yellow to brown, as were most shells from Bet Hillel. In Sede Nehemya and the Eastern Canal the shells were nearly black. At Upper Jordan outlet, Gesher Benot Ya'aqov and En Yezer shell colour was more variable - from greyish yellow to black or reddish brown. At six sites some shells were banded, the bands varying in colour and width. At Bet Hillel (the two sites combined) 11% of the shells were banded, at Gesher Benot Ya'aqov 20%, at En Yezer 10% and at Jordan inlet into Lake Kinneret, 33%.

Habitat   River banks where the current is weak. *M. c. costata* inhabits silty mud, submerged vegetation, and is sometimes found a few cm above water.

Geographic range and habitat   In the upper Jordan River, from Bet Hillel to Lake Kinneret. It occurs also in the lower Jordan River.

Today *c. costata* has a narrow, linear distribution (from Bet Hillel directly down to Lake Kinneret). Merely forty years ago its dominant habitats in our study area used to be the Hula Lake and the vast Hula swamps, that were drained in 1958. The total area of this lake and its swamps used to fluctuate annually between 21 km² (summer) and 60 km² (winter); and whereas the lake occupied a fairly stable surface area of 14 km² (its depth was 1.5–2.5 m), the swamps changed to a much greater extent (Dimentman, Bromley & Por, 1992).

Comparisions   In addition to being ribbed, *M. c. costata* (n = 140) differs from *M. buccinoidea* (n = 240) in having significantly lower values of the ratios shell-diameter / shell-height, mouth-height / shell-height and mouth-height / shell-diameter; and higher values of the ratios mouth-diameter / mouth-height, notch-width / mouth-diameter and notch-depth / mouth-diameter (P < 0.01).

Our *c. costata* are similar to Olivier's original figure of *costata* from the Orontes (Gesser ech Chegueur, northern Syria). They are further similar to the cotype of *cerithiopsis* illustrated by Pallary pl. 4 Fig. 10; to his *M. germaini* illustrated in pl. 6 Fig. 8 and to *saulcyi* in his pl. 6 Fig. 27 and pl. 6 Fig. 29.

Remarks   Much of the lower Jordan River (south of Lake Kinneret) is inaccessible but we did succeed in collecting one sample from the lower Jordan (south of the Allenby Bridge, IG 201138). The Allenby Bridge shells (Fig. 4C, lower Jordan) differ from *c. costata* of the upper Jordan in that they are significantly more narrow (shell-diameter / shell-
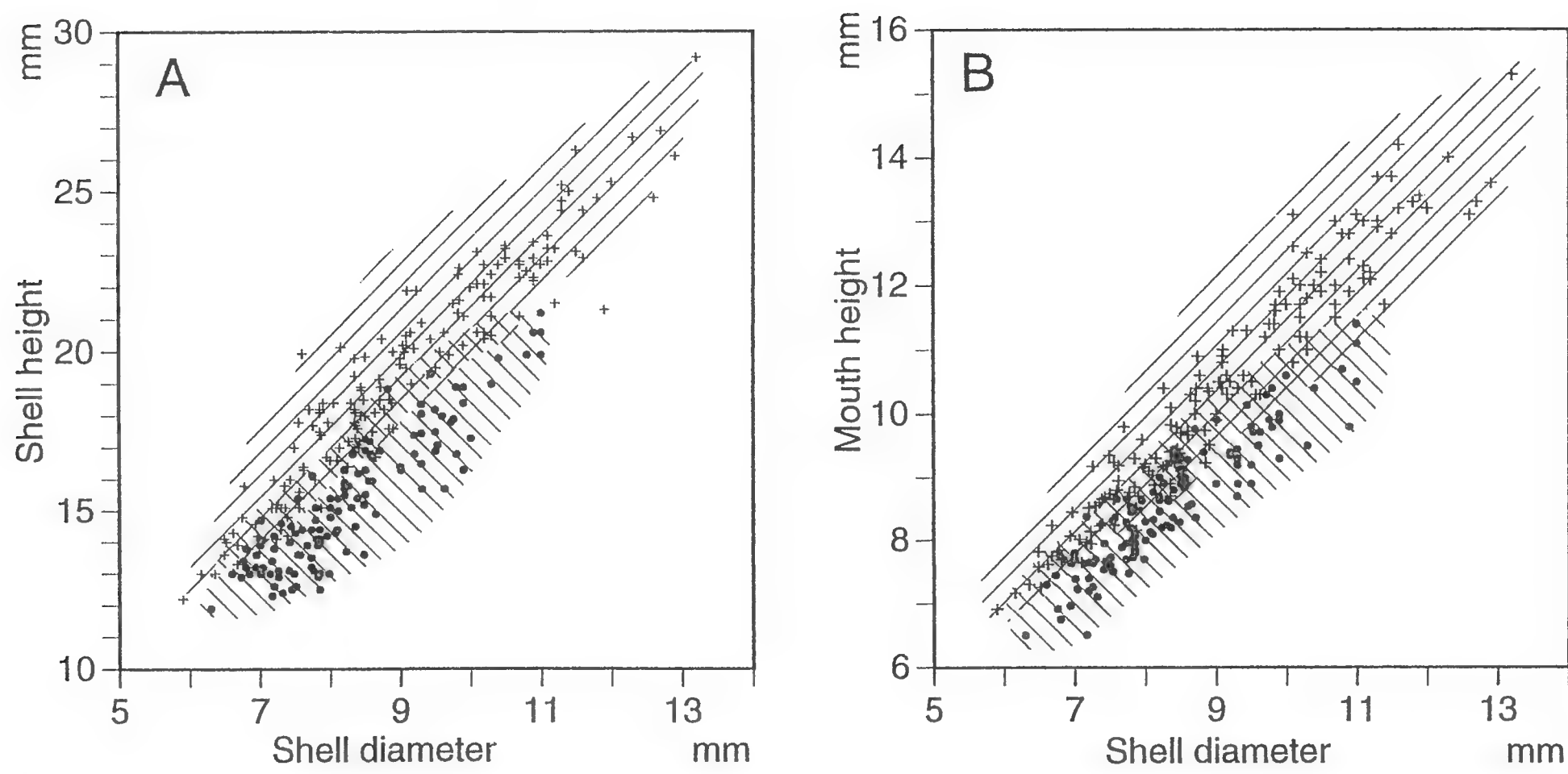
Fig. 8   *M. costata costata* (+) and *M. costata jordanica*   (●): **A** Shell-height versus shell-diameter. **B** Mouth-height versus shell-diameter.

height = 0.43±0.2) and have a smaller aperture (mouth-height/shell-height = 0.49±0.03). We are undecided as to whether they should be assigned to *c. costata* or to some other subspecies.

In Lake Kinneret (between *c. costata* of the upper Jordan and Allenby Bridge shells of the lower Jordan) another subspecies occurs, *M. c. jordanica*.

Melanopsis c. jordanica Roth.
Fig. 4D.

Melanopsis costata var. *jordanica* Roth 1839: 25; Pl. 2, Figs 12 and 13.
Melanopsis costata var. *jordanica* Roth 1855: 38.
Melanopsis Jordanica Blankenhorn1897, Pl. 10, Figs 20–21.
Melanopsis jordaniensis Germain, 1921.
Melanopsis praemorsum Tchernov 1975: Figs 1–2.

Holotype and Type locality   *Melanopsis costata* var. *jordanica* from 'mari Galilaeo", type specimen in München Museum.

Material examined   En Sheva, Ginnosar, En Raqqat, En Gev, Haon, Bet Gavriel, Kinneret 208.

Measurements

Shell Character	Range	Mean ±S.E.
shell-height	up to 20.6 mm	
shell-diameter	up to 11.0 mm	
mouth-height	up to11.4 mm	
mouth-diameter	up to 5.1 mm	
notch-width	up to 3.0 mm	
notch-depth	up to 3.4 mm	
shell-diameter / shell-height	0.48–0.63	0.541 ± 0.010
mouth-height / shell-height	0.46–0.66	0.557 ± 0.008

mouth-diameter / mouth-height	0.39–0.61	0.456 ± 0.007
mouth-height / shell-diameter	0.90–1.34	1.032 ± 0.013
notch-width / notch-depth	0.73–1.07	0.906 ± 0.016
notch-width / mouth-diameter	0.35–0.78	0.522 ± 0.007
notch-depth / mouth-diameter	0.37–0.80	0.577 ± 0.012
number of ribs	8–14	10.842 ± 0.277
rib form	1–2	1.608 ± 0.071
rib length	3–4	3.725 ± 0.063
rib index	3.6–6.6	5.044 ± 0.148

(Overall measurements. Detailed measurements of the different samples are in Appendix 1C).

Description M. c. *jordanica* differs from c. *costata* in that its shell is usually more stout. The ribs are mildy pronounced, and their shoulders are rounded. Shell colour varies: Some shells are black but many other shells are banded, the dark bands being broad and black, the pale bands narrow and pale grey to dark brown. The ultimate whorl of each shell has three dark bands and two pale ones.

The frequency of banded shells varied between the different sites: at En Sheva and Ginnosar 10%, at En Raqqat 80%, at En Gev 88%, at Haon 16%,, and at Bet Gavriel 8%. On each shell the contrast between the dark and the pale bands was usually greater than in c. *costata* and *buccinoidea*. At all sites the non-banded shells were uniform black or brown.

Raanan (1986) found that in some Kinneret populations shell height increases with depth, from shoreline down to 3 m; our collecting was restricted to the shoreline.

Habitat and Geographic range M. c. *jordanica* is found in Lake Kinneret (170 km²), which differs from the Jordan in its frequent storms. Daily from April to October, a western breeze from the Mediterranean Sea reaches the Kinneret at about noon. This breeze causes the lake to become wavy, choppy or stormy until late in the evening. From December to mid-March there is no western breeze, but strong eastern winds from the Syrian desert (the 'Sharkiyeh") then frequently reach the lake causing similar effects (Heller, 1979a). Two snail-predating fish, *Barbus longiceps* and *Blennius fluviatilis*, are found in Israel mainly in Lake Kinneret (Heller, 1979a); they may perhaps exert some selection on shell colours. M. c. *jordanica* occurs only along rocky shores of the Kinneret, consisting of gravel, cobble, stones and boulders; and is not found on muddy shores consisting of muds, sands and silts. It occurs down to a depth of 5 m (Tchernov, 1975a; Raanan, 1986). Raanan (1986) found that banded snails are more common on the tops of rocks while black snails are more common underneath. He also found that juveniles occur mainly in shallow, rather than deep water.

In its natural condition the water level of Lake Kinneret used to fluctuate annually at an average of 0.80–1.00 m (maximum 1.50 m). In 1932 the Kinneret was dammed and its outlet deepened to construct a hydro-electrical plant, and from that year onwards annual fluctuations in the water level increased to 3 m. In 1964, when the lake became Israel's major reservoir, its level was increased by 1 m; and was left at peak levels for much longer periods than in its natural condition (Nun, 1977). Further, in its natural condition the lake's salinity was almost 400 mg/l (chlorinity). Recent diverting of haline springs from the lake has decreased its salinity to about 200 mg/l (Nun, 1977). Today's major habitat of *jordanica* is thus very disturbed. Beyond Lake Kinneret, *jordanica* occurs in the upper reaches of the lower Jordan River, from the exit of Lake Kinneret another 2 km downstream, to Deganiya (beyond which the Jordan is polluted and no *Melanopsis* are found for quite a distance). Specimens in the National Mollusc collection record its

presence also 30 km downstream (Dalhamya, Shifa).

Our observation that *c. costata* occurs in the upper Jordan whereas *jordanica* occurs in the Kinneret agrees with Tristram (1865: 542) who "never met *costata* south of the entrance to the Lake of Galilee in a living state, nor *jordanica* to the north of it".

Comparisions   That *M. c. jordanica* (n=120) is stouter than *c. costata* (n=140) is expressed in higher values of the ratio shell-diameter / shell-height (P < 0.01). Further differences concern the higher ratio mouth-diameter / mouth-height (P < 0.05), lower ratio mouth-height / shell-diameter (P < 0.01), higher Rib-index (P< 0.01), and higher rib length (P < 0.05). Maximal shell-height of *c. jordanica* is only 65% that of *c. costata*, in this study (Fig. 8). *M. c. jordanica* differs from *M. buccinoidea* in all shell ratios (P < 0.01), except notch-width / notch-depth.

If we plot shell height versus shell diameter of *costata*, and consider the area encircling the resulting scatter diagram as its 'morpho-space'; and if we similarly create a morpho-space for *jordanica*; then 16.8% of the morpho-space of costata overlaps with *jordanica*, and 26.7% of the morphospace of *jordanica* overlaps with *costata* (Fig. 8A). If we plot mouth height versus shell diameter in these two subspecies, then 20.6% of the morpho-space of *costata* overlaps with *jordanica*, and 40.3% of the morphospace of *jordanica* overlaps with *costata* (Fig. 8B).

Remarks   We base the assigning of the Lake Kinneret *costata* to *jordanica* upon comparision with the type specimen in München, and also with Roth's (1839, pl. 2 Figs 12–13) description, measurement and figure of what he described as *Melanopsis costata* var. *jordanica*, from 'mari Galilaeo'. Germain (1921–2) placed *M. jordaniensis* under a separate heading, but noted that it is close to *costata*, and may perhaps be merely a *costata* variety. He described it as having a short, stout shell with yellow bands, and echoed Tristram's (1865) comment that whereas *costata* inhabits submerged vegetation, *jordaniensis* is found only on stones. Our own observations support both his description and his remark concerning the habitats of these two taxa. Pallary (1939) illustrated *Melanopsis cerithiopsis* from 'de Genezareth' (pl. 6 Figs 49–50); this narrow form with ribs consisting of tubercles was never found by us in Lake Kinneret (we found it 7 km further southeast). There could perhaps be errors in the localities of Pallary, who did not collect his Kinneret material himself. The *M. praemorsum* described by Tchernov (1975a, Figs 1–2) are typical *jordanica*. Raanan (1986) suggested that the black and banded morphs of *M. costata* of Lake Kinneret may belong to two separate species, with incomplete reproductive isolation. However conchiometric and electrophoretic studies do not support this suggestion (Marko, 1984; Altman & Ritte, 1996).
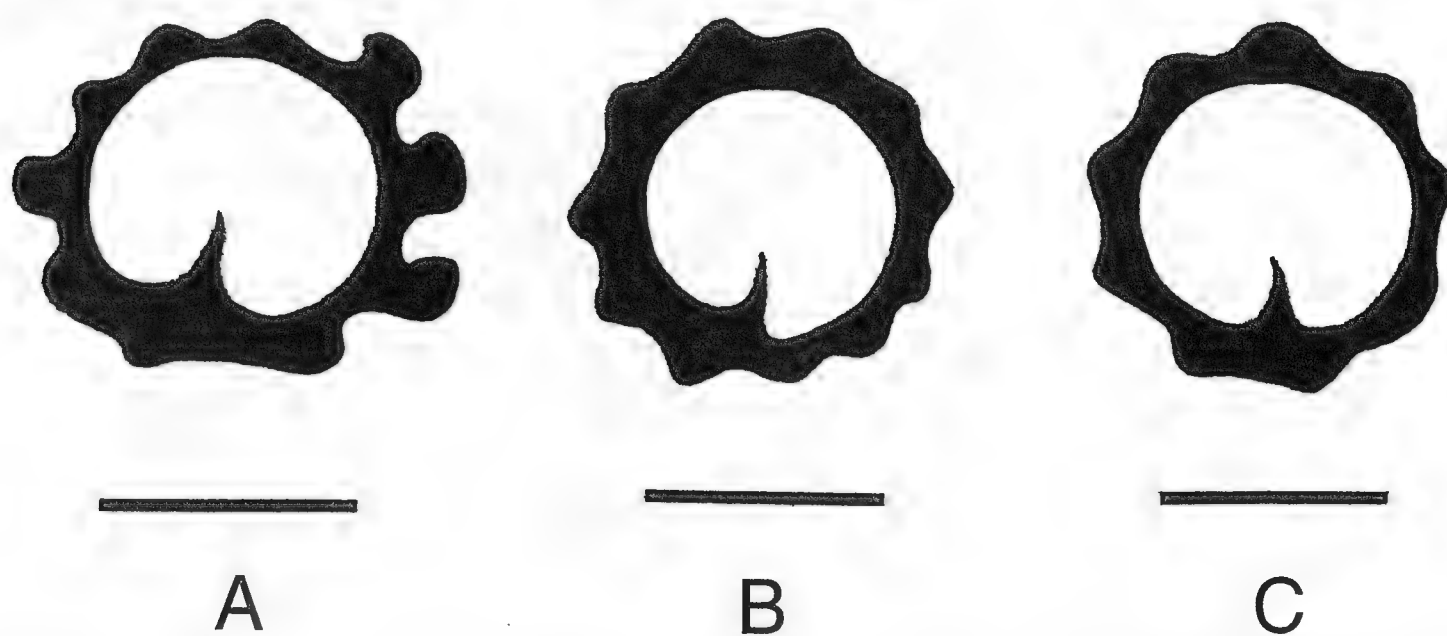

A   **B**   **C**

Fig. 9   Rib-height in typical *M. c. noetlingi* (Yarmouk) (**A**) *M. c. costata* (Sede Nehemya) (**B**) and *M.c. jordanica* (En Raqqat) (**C**) in transected shells.

In the small, 1 km-long section of the north-eastern shores of Lake Kinneret, from the Upper Jordan outlet to the Nahal Meshoshim outlet, shells intermediate between *c. jordanica* and *costata* were found (Appendix 1 D, compare the ratio shell-diameter / shell-height to *costata,* Appendix 1B and to *jordanica,* Appendix 1C). This small stretch has undergone considerable changes since the draining of the Hula in 1958: large quantities of sediment that once used to be deposited in the Hula today reach the Kinneret where they have created a rapidly expanding delta, into which the river bed of the Jordan now extends about 1 km eastwards, towards the Nahal Meshoshim outlet (Nun, 1977). It is noteworthy that among 35 samples of Lake Kinneret whose isozymes were examined by Altman & Ritte (1996), their two samples from Nahal Meshoshim outlet had the lowest average genotypic similarity. Their evidence (based upon electrophoresis) supports our suggestion (based on conchiometrics) that the Meshoshim outlet population differs from other populations of Lake Kinneret (which are *jordanica*) in that it is intermediate between *jordanica* and *costata.* The *M. praemorsum* illustrated by Tchernov (1975a) in his Figs 3–4 and 7–8 are typical intermediates. One of Pallary's figures of cerithiopsis (pl. 4 Fig. 9; not his other *cerithiopsis*), two of his figures of *saulcyi* (pl. 6 Figs 15 and 30) and one of his figures of *orontis* (pl. Fig. 72; not his other *orontis*) seem somewhat similar to our *costata-jordanica* intermediates.

In the lower reaches of the lower Jordan another shell occurs, *M. c. noetlingi.*

Melanopsis c. noetlingi Bourguignat
Fig. 4E.

Holotype   *Melanopsis noetlingi* Bourguignat, in Noetling 1886, p. 817; Plate 23, Fig. 6.

Type locality   Yarmouk bei el Hammi.

Material examined   Yarmouk (IG 210232), about 1 km from type locality.

Measurements

Shell Character	Range	Mean ±S.E.
shell-height	up to 0.4 mm	
shell-diameter	up to 10.8 mm	
mouth-height	up to 10.6 mm	
mouth-diameter	up to 4.8 mm	
notch-width	up to 3.5 mm	
notch-depth	up to 4.2 mm	
shell-diameter / shell-height	0.48–0.59	0.54 ±0.02
mouth-height / shell-height	0.46–0.57	0.52 ± 0.03
mouth-diameter / mouth-height	0.46–0.51	0.46 ± 0.02
mouth-height / shell-diameter	0.88–1.06	0.98 ±0.06
notch-width / notch-depth	0.70–1.03	0.86 ± 0.08
notch-width / mouth-diameter	0.55–0.83	0.70 ± 0.07
notch-depth / mouth-diameter	0.67–0.95	0.816 ± 0.07
number of ribs	9–12.5	0.93 ±1.05
rib form	1–4	2.83 ± 1.22
rib length	4	4.00 ± 0.00
rib index	4.08–5.78	4.95 ± 0.05

Description   *M. c. noetlingi* differs from *c. costata* of the upper Jordan and *c. jordanica* of the Kinneret in that the ribs on the ultimate whorl are very high and prominent. Each rib consists of a very prominent upper tubercule, fused to a straight, prominent, lower
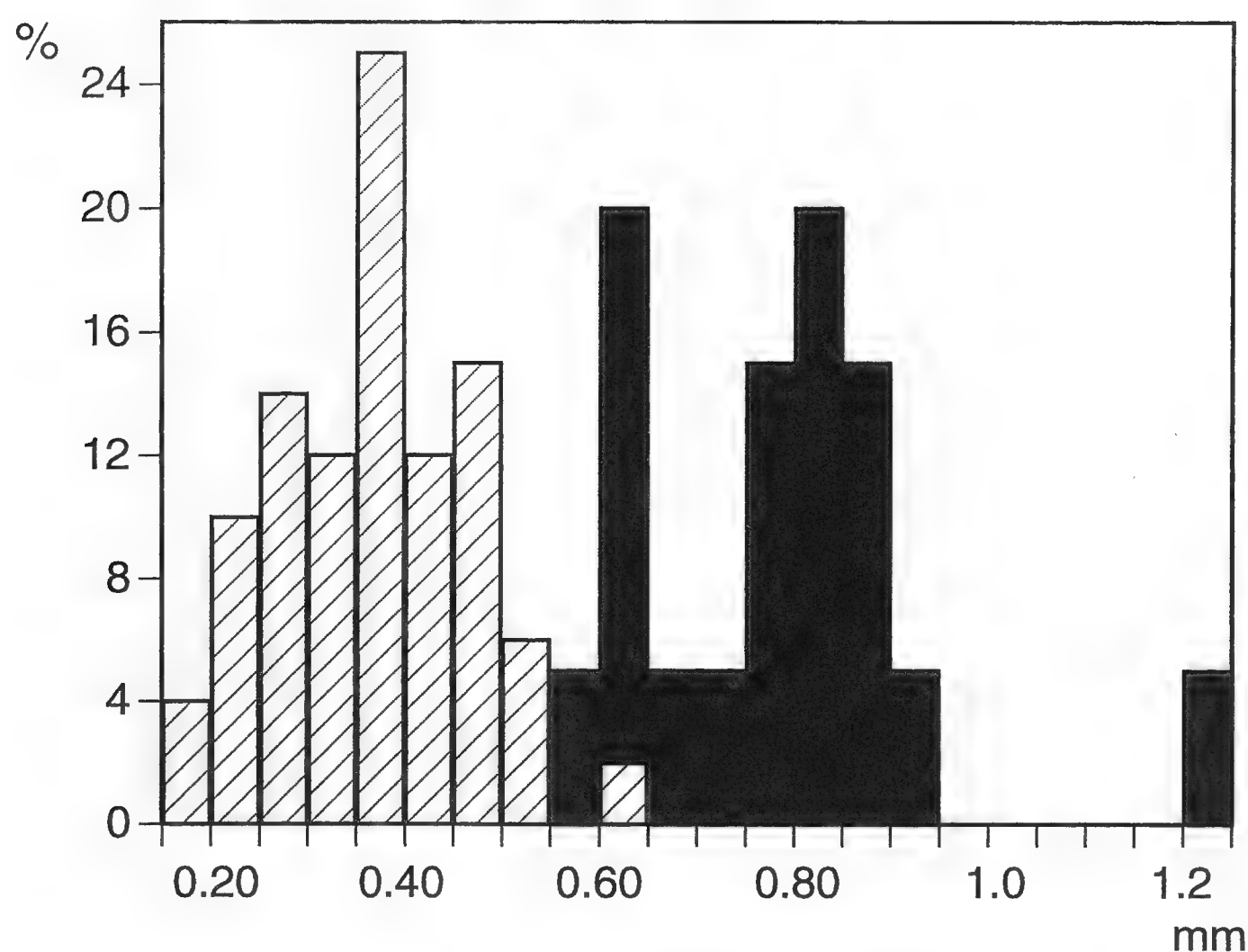
Fig. 10   Rib-height frequency in *M. c. noetlingi* from the Yarmouk (black, n=20) and in *M. c. costata* + *M.c. jordanica* (hatched, n=50) pooled from varous sites.

ridge. The tubercle and the ridge are either continous, or separated by a depression.

Habitat   On boulders near the bank of the river.

Geographical range   The Yarmouk, near its outlet into the Jordan. Elsewhere the Yarmouk is inaccessible to us.

Comparisons   Rib height in *M. c. noetlingi* is significantly higher than in both pooled and separate samples of *c. costata* and *c. jordanica* (t test, P< 0.001; Fig. 9 and Fig. 10); no significant difference was found between *c. costata* and *c. jordanica*. In the shells that served to measure rib height also shell-diameter was measured (it ranged from 6.2 to11.2 mm); no correlation was found between shell-diameter and rib-height.

Remarks   Noetling sent (recent) shells from 'Yarmouk bei el Hammi' to Bourguignat, who described them as a separate species, *noetlingi*. Bourguignat did not illustrate *noetlingi* but the figures of Noetling (1886) leave no doubt that the shells he collected at this site are similar to those collected by us. Blanckenhorn & Oppenheim (1927) redescribed *noetlingi*. However, both from their illustration (pl. 21 Figs 12–13, and from inspection of their material, it could well be that their specimens should be assigned to another taxon.

<div align="center">

Melanopsis saulcyi Bourguignat 1853
Fig. 4F, 4G

</div>

Melanopsis saulcyi Bourguignat 1853
Melanopsis saulcyi Germain 1921.
Melanopsis cerithiopsis Pallary 1939.

Holotype   *Melanopsis saulcyi* Bourguignat 1853: 66, pl. 2 Figs 53 and 54.

Type locality   "Artouse, en Syrie" (Bourguignat 1853: 66).

Material examined   Hammat Gader, Ma'ayan Harod, Enot Huga, Gan Hashelosha, Sheluhot, En HaNaziv, Sede Eliyyahu, En Hamma.

Measurements

Shell Character	Range	Mean ±S.E.
shell-height	up to 26.0 mm	
shell-diameter	up to 12.3 mm	
mouth-height	up to 12.5 mm	
mouth-diameter	up to 5.5 mm	
notch-width	up to 4.0 mm	
notch-depth	up to 5.1 mm	
shell-diam / shell-height	0.37–0.55	0.448 ± 0.009
mouth-height / shell-height	0.38–0.60	0.503 ± 0.010
mouth-diam / mouth-height	0.37–0.51	0.446 ± 0.004
mouth-height / shell-diameter	0.86–1.33	1.132 ± 0.007
notch-width / notch-depth	0.50–1.14	0.811 ± 0.013
notch-width / mouth-diameter	0.24–0.60	0.425 ± 0.001
notch-depth / mouth-diameter	0.36–0.70	0.525 ± 0.002
number of ribs	9–19	12.719 ± 0.305
rib form	1–4	2.734 ± 0.200
rib length	2–4	2.916 ± 0.183
rib index	2.42–5.0	3.573 ± 0.106

(Detailed measurements of the different samples are given in Appendix 1 E.)

Description   The shell is almost always elongate and slim, and its aperture is small, in relation to shell-height. The 2–4 upper whorls are smooth (in our samples, very frequently they are eroded), the 3–6 lower whorls are ribbed. In most shells the ribs descend from the suture until about the middle of the lowest whorl; in others they descend further, sometimes to the base of the whorl. Usually each rib consists of an upper tubercule, fused to a lower ridge. When the ribs extend the entire height of the lower whorl this is due not to a simple extension of the existing ridge downwards, but to the appearance of an additional ridge, beneath the previous (upper one); eventually the two ridges fuse, to a varying extent; the overall appearance of the shell in this case is 'bumpy' and the lower ridge of the ribs bend leftwards, towards the base of the columella. In some shells the ribs are simple, not tuberculate.

The sutures are wavy. The notch is deep. Shell colour (beyond the upper, frequently eroded whorls) varies from uniform dark brown to uniform black. In some of the shells the upper part is black and the lower part dark reddish brown. On the inner lip the pale callus of the upper parietal wall merges with the white columella, so the entire inner lip is pale.

Habitat and Geographic range   We found *saulcyi* in springs and streams, from Hammat Gader (south-east of Lake Kinneret) southwards, via Bet Shean Valley to En Hamma (Fig. 11). It was also found in Jericho (Ein Sultan). Museum specimens collected at the turn of the century offer evidence that it then extended further north, along the margins of the (today dried) Hula swamp. It is our impression that, up to the turn of this century, the original habitat of this species used to be streams that border swamps; today no swamps are left.

Beyond our study area Schütt (1987, 1988b) described and illustrated *Melanopsis prae-*
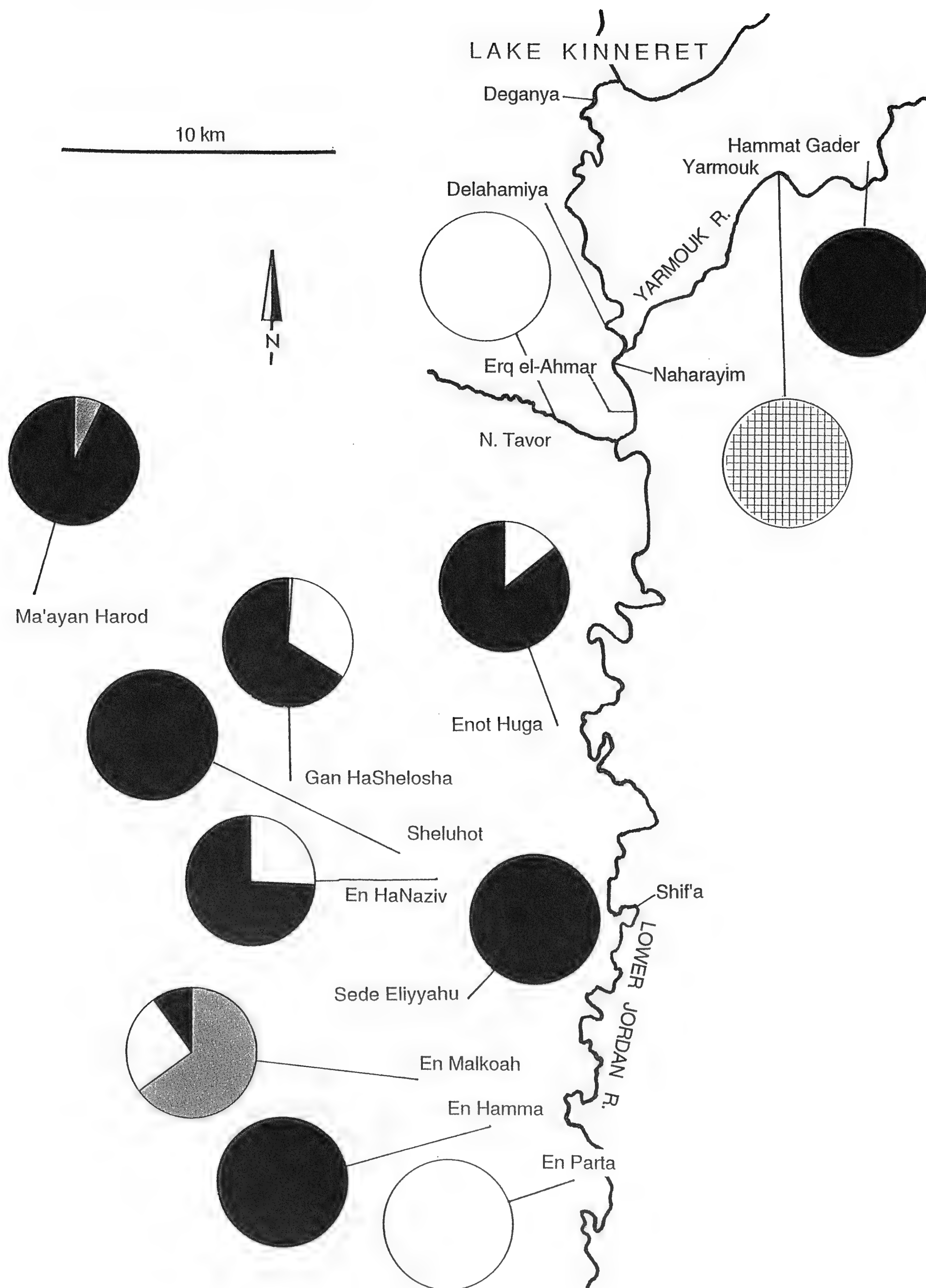
Fig. 11 Frequency of *M. buccinoidea* (white), *M. saulcyi* (black), intermediates (gray) and *M. noetlingi* (cross-hatched) in samples of the area south of Lake Kinneret.

morsa obsoleta Dautzenberg 1894 from Palmyra oasis, in Syria; this shell is very similar to *saulcyi*.

Comparisons   M. *saulcyi* differs from *buccinoidea* in that it is ribbed, more slim (lower ratio shell-diameter / shell-height), has a smaller mouth (lower ratio mouth-height / shell-height) that is more roundish (higher ratio mouth-diameter / mouth-height), a lower ratio mouth-height / shell-diameter and a lower ratio notch-width / notch-depth (all differences significant at P <0.01; in addition, the ratio notch-width / mouth-diameter differs at P < 0.05).

It differs from *costata jordanica*, which is ribbed, in that its shell is much slimmer (the ratio shell-diameter / shell-height is lower, the ratio mouth-height / shell-diameter higher), has a smaller aperture (the ratio mouth-height / shell-height is lower), the notch is more deep (the ratio notch-width / notch-depth is lower), the ratio notch-width / mouth-diameter is lower and its number of ribs higher, the frequency of tubercles on the ribs is higher, and the rib length and the rib index are lower (all differences significant at P <0.01; in addition, notch-depth / mouth-diameter differs at P < 0.05). It further differs in that it does not contain banded shells, common in *c. jordanica*.

It differs from *c. costata* in that it has a smaller aperture (the ratio mouth-height / shell-height is lower); the ratios notch-width / notch-depth, notch-width / mouth-diameter and notch-depth / mouth-diameter are lower, number of ribs higher, the frequency of tubercles on the ribs is higher, rib length and the rib index lower (all differences significant at P <0.01; in addition, the ratio shell-diameter / shell-height differs at P < 0.05).

Remarks   At five sites *saulcyi* was found together with M. *buccinoidea*: Enot Huga, Gan HaShelosha, En HaNaziv, En Malkoah and Ein Sultan. At two of these sites intermediates, characterized by shallow ribs, deep sutures and slim proportions, were found. At Gan Hashelosha we examined 150 shells. Of these 67% were *saulcyi*, 33% were M. *buccinoidea* and only one shell was intermediate. At En Malkoah 10% of the shells were *saulcyi*, 25% M. *buccinoidea* and 65% were intermediate. At Ma'ayan Harod 83 shells were examined, of these 7% were intermediate and all the rest were *saulcyi*. At En HaNaziv 74% were *saulcyi* and 26% *buccinoidea*; at Enot Huga 86% were *saulcyi* and 14% *bucci-*
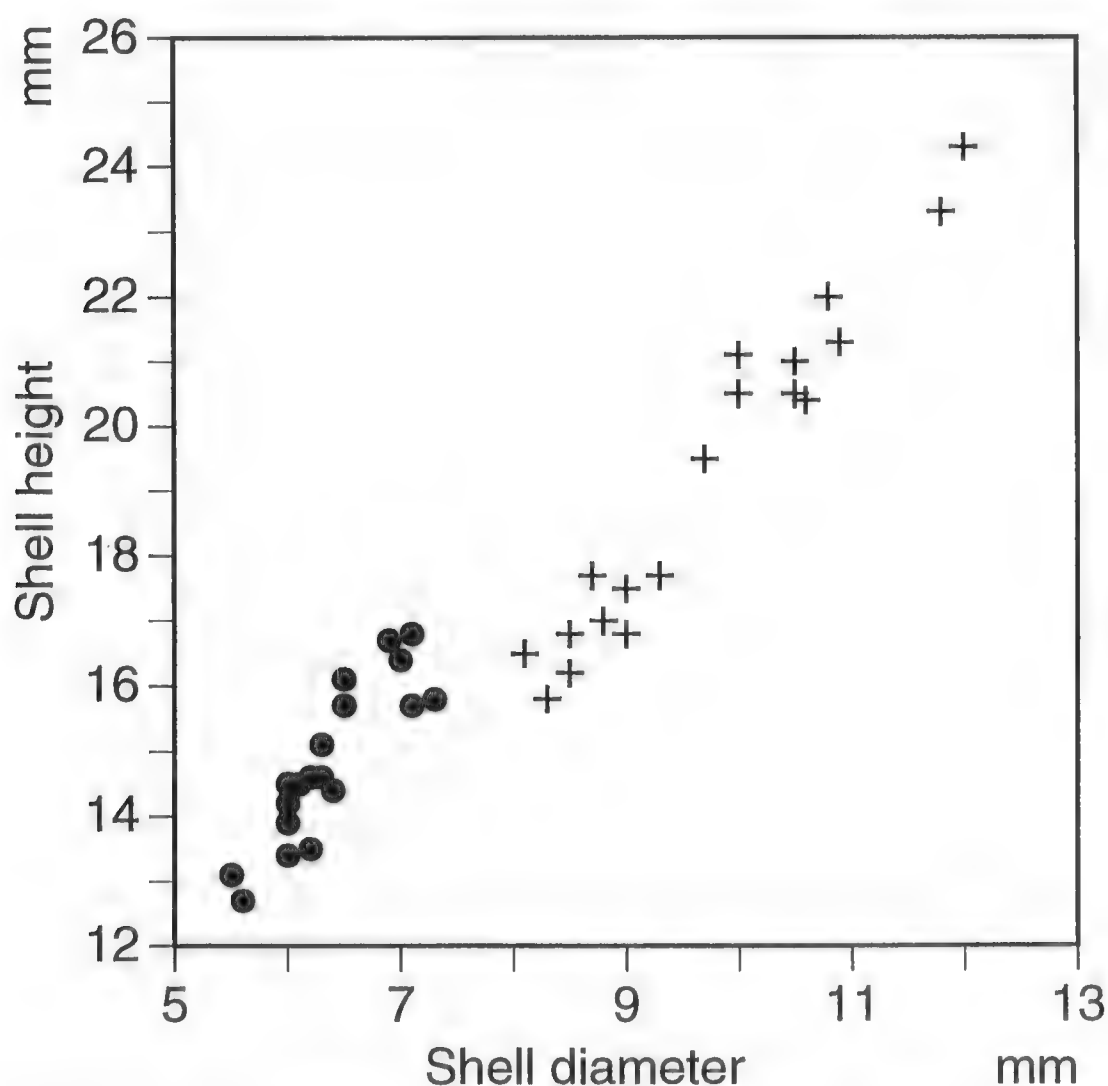

Fig. 12   Shell-height versus shell-diameter of *saulcyi* (•) and *buccinoidea* (+) ; all specimens from within a 2 m radius at Ein Sultan (Jericho).

noidea. At Sheluhot, Sede Eliyyahu and En Hamma all the shells were typical *saulcyi*. Fig. 12 illustrates the different shell conchiometrics (shell-height versus shell-diameter) of *saulcyi* and *buccinoidea* found together within a 2 m radius at Ein Sultan (Jericho); no hybrids were found.

Considerable variation was found in rib length and form. Enot Huga had the shortest ribs, Sheluhot the longest (and fewest) ones. In Sheluhot most shells also had distinct tubercles, whereas at the other sites some of the shells had uniform ribs. The tubercle near the suture frequently appears to be formed as an outwards detour of the outer lip, to avoid the well-developed callus of the inner lip.

Variation was also found in shell height. At Hammat Gader, in a pond 20 m downstream from the source, mean shell height was 14.7 mm + 1.3; a few hundred m further downstream, in a canal between fish ponds, it reached 21.0 mm + 3.0. This large size may be related to the fact that the water in the canal was rich in nutrients, from the nearby fish ponds. Also, at the source of Hamat Gader 95% of the shells were eroded whereas at the pond (and in the canal) none were.

Sheluhot, En HaNaziv, Sede Eliyyahu and En Hamma had slim shells (low ratio shell-diameter / shell-height), Ma'ayan Harod and Enot Huga had stouter ones. Sheluhot and Sede Eliyyahu had completely black shells, at the other sites part of the shells were dark reddish brown (they were always darker than *M. buccinoidea* from the same site).

Discussion Tristram (1865: 542) mentioned *saulcyi* from Ain Sultan, Jericho. Dautzenberg mentioned it (1894: 17) from Et-Tell: Gué du Jourdain; and a var. *maxima* from Bir Jaloud. Germain (1921–2) described *M. saulcyi* as having ribs that in the upper whorls are well-developed, but in the final whorl extend only along the upper half (the lower half of the whorl is smooth). However, he noted that in some *saulcyi* shells the ribs occupy three quarters of the last whorl. He mentioned *saulcyi* from Tartouse and Palmyra (in Syria), and from Bir Jaloud, Jericho, and Jordan near the Dead Sea (in our study area).

Also Pallary (1939) described *saulcyi* as having ribs that do not reach beyond the upper part of the last whorl. However, he commented that it is found only in Syria (Tripoli, Tartouse, Lake Antioch, Lake Homs, Nahr el Kebir, Jeni Schehir), since previous records from Palestine are misidentifications. Another species, *M. cerithiopsis* Bourgignat 1884, was described by Pallary (1939) as having ribs that reach down to the base of the last whorl, and as sometimes having two rows of granulations in each whorl; usually these granulations combine to form ribs. However, he noted that in *cerithiopsis* var. *mezeribensis* the ribs do not reach the base of the whorl; and that in *cerithiopsis* var. *emaciata* the granulation is barely visible and the ribs are straight. He illustrated the types from the collection of Bourguignat, and additional specimens of this species from Ain Mallaha (today Enot Ennan), Lake Kinneret ('de Genezareth'), Bir Jeloud (today En Harod) Sachne (today Gan Hashelosha), Jericho, and Mezerib.

M. saulcyi is thus described as having simple ribs that usually do not reach beyond the upper part of the last whorl, *M. cerithiopsis* as having (sometimes granulated) ribs that usually reach down to the base of the last whorl. Within our samples from Ma'ayan Harod and Gan Hashelosha (and to a certain extent also En Hamma) rib length varies from half to the entire extent of the last whorl; and granulation (expressed in terms of a 1–4 scale) varies from distinct bumps to simple ribs. In only one of our samples, Sheluhot, do most shells have ribs that reach down to the base of the last whorl. Because of this continuous variation in rib length and form, we consider *cerithiopsis* a synonym of *saulcyi*.

DISCUSSION

Melanopsis is a key genus in many studies concerning systematics, parasitology, ecology, palaeontology and evolution (an exhaustive list of references concerning *Melanopsis* is presented by Glaubrecht 1996). The Jordan Valley is rich both in highly variable Recent *Melanopsis* and in fossil sediments (in which *Melanopsis* is very abundant). Hence the need for a detailed systematic study on *Melanopsis* from the Jordan Valley.

This study reveals three morphologically distinct entities of *Melanopsis* in the area under study. We consider *buccinoidea*, *costata* and *saulcyi* to be separate species, due to the considerable diagnostic conchological differences between them.

In zones of contact these species largely remain distinct. Hybrids are found in over-lapping zones of no more than a few hundred m, and at low frequencies. This suggests that the species maintain their distinct genetic integrities, and that the narrow hybrid zones act as substantial, but not absolute barriers to gene flow. We feel that when hybrid zones are very narrow, hybridization need not conflict with the recognition of geographic forms as different species; Already Darwin (1872, vol. 2: 17) recognized that sterility among hybridizing animal species is not an absolute and universal trait.

Tchernov (1975b) notes that the smooth and costated *Melanopsis* interbreed, at sites where small water bodies reach the shore of Lake Kinneret. Situations comparable to *Melanopsis*, where taxa maintain their integrity yet hybridize at the edge of their geographical or ecological distributions, have been found in a variety of animals, includ-ing mammals, birds, amphibians, reptiles, orthopterans and butterflies (Grant & Grant, 1992; Harrison, 1993; Werner & Watson, 1996; Jiggins et al. 1996). Among gastropods however, only few cases of hybrid zones have been reported. A hybrid zone of 1–5 km extends along the borderline between the land snails *Levantina caesareana* and *L. hierosolyma* in Israel (Heller, 1979b), and of 5 km between the land snails *Manadarina mandarina* and *M. chichijimana* in the Bonin Islands (Chiba, 1997). Among freshwater snails, *Elimia livescens* was found to hybridize with *E. virginica* (Bianchi, Davis & Strayer 1994).

We suggest that the populations from the Jordan, Lake Kinneret and the Yarmouk are subspecies of *costata* (*c. costata*, *c. jordanica* and *c. noetlingi* respectively) rather than distinct species, because the differences between them are not fully diagnostic, even though statistically significant. Wilson & Brown (1953) feel that subspecies are not objec-tively definable, and suggest that systematics should get rid of the subspecies category. In this present study, discarding of the subspecies category would mean ignoring the fact that a large geographical fraction of the species (almost all Lake Kinneret) has a significantly different shell morphology: Shells that are stout beyond a certain degree are found exclusively in the Kinneret; shells that are narrow beyond a certain degree are never found in the Kinneret (intermediate shells are found both in the Kinneret and else-where); shells with ribs that are very high are found exclusively in the Yarmouk. In other words, to a certain extent intraspecific shell variation is predictive in geographic (and, for the Kinneret, in habitat) terms. Electrophoresis would be clearly required to add further support to our suggestion concerning the subspecies status of these three geographic variants.

Within *buccinoidea*, shells from Nahal Dan differ in their shallow notch and small mouth-height; and within *costata*, shells from Allenby Bridge differ in being narrow and having a small mouth-height. We cannot decide whether these conchological differences justify separation of these snails into different taxa.

Tchernov (1975a,b) suggested that the ribs of *costata* may be an adaptation to stormy habitats. This was rejected by Glaubrecht (1993). We too do not see a correlation between costation and a stormy habitat. By and large, *buccinoidea* is a dweller of fresh springs, trickles and small streams with a bottom of gravel or boulders, whereas *costata* seems to

represent habitats that (at least untill recently) were either swamps with a muddy bottom, or large rivers with muddy banks, or lakes with rocky shores.

The small, stout shell of *c. jordanica* (as compared to *c. costata*) correlates with a stormy habitat. Also among British rock-dwelling winkles, shells from exposed shores are smaller and more globose than those from sheltered shores (Heller, 1976). A stout, globose shell could accomodate more foot muscle and thus enable a stronger adherence to rocks and boulders during severe storms. In Canadian *Littorina obtusata*, where wave exposed snails are similarly smaller, more squat and have larger foot sizes than those of protected habitats, increased hydrodynamic stress was found to induce a plastic increase in foot sizes (Trussel, 1997). This may also be the case in *c. jordanica*, the stout shell being a phenotypic response to the stormy environmental conditions of Lake Kinneret. However, Raanan (1986: 64, Table) bred stout snails of the Kinneret in laboratory conditions and found that the progeny were exclusively stout; and a sample of *c. jordanica* collected by us from the sheltered harbour of En Gev (SD/SH = 0.53± 0.02; MH/SD = 1.04 ± 0.04) did not differ in shape from a pooled sample of all *c. jordanica* in this study, all from exposed shores of Lake Kinneret. This suggests that differences in shell shape between *c. jordanica* and *c. costata* are genetic.

As mentioned in our Introduction, taxonomic analysis may get out of hand when overall variation of a very large geographic region is considered simultaneously; a more cautious approach may be to start by developing a conchiometric taxonomy that concerns only one small region, and only later to extend research. Accordingly, this conchiometric study of Recent *Melanopsis* in the Jordan Valley presents our first stage in a more comprehensive research. Future research will expand the range of characters into sperm morphology (e.g. Hodgson & Heller, 1997 and in prep.) and isozymes (Falniowski, Szarowka & Heller in prep.). It will also expand the geographic range of study, gradually to encompass *Melanopsis* of neighbouring regions (the Judean Desert, Israel's coastal plain and the state of Jordan); and investigate fossil *Melanopsis* of the Jordan Valley (Heller & Sivan in prep.).

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Appendix 1 A. Measurements (mm) and ratios of the twelve samples of *M. buccinoidea* (mean ± S.D., and observed range).

MEASUREMENTS (mm)

	Shell height	Shell diameter	Mouth height	Mouth diameter	Notch width	Notch depth
Nahal Dan	18.70 ± 1.36	8.93 ± 0.59	10.06 ± 0.87	4.30 ± 0.32	2.24 ± 0.21	2.02 ± 0.30
	17.1 - 21.6	8.1 - 9.9	8.4 - 11.7	3.8 - 5.0	1.8 - 2.4	1.4 - 2.8
Nahal Senir	20.09 ± 2.02	9.88 ± 1.09	11.57 ± 1.18	4.79 ± 0.54	2.30 ± 3.08	2.55 ± 0.36
	17.6 - 26.0	8.4 - 13.2	10.0 - 15.2	4.0 - 6.3	1.8 - 3.0	2.0 - 3.5
Bet Hillel N	20.31 ± 1.18	10.18 ± 0.73	11.86 ± 0.86	4.99 ± 0.30	2.30 ± 0.37	2.50 ± 0.32
	18.3 - 22.4	8.7 - 11.6	10.5 - 13.7	4.3 - 5.6	1.7 - 3.1	1.9 - 3.2
Nahal Gilbon	20.82 ± 1.83	10.49 ± 1.06	12.88 ± 1.19	5.12 ± 0.46	2.03 ± 0.36	2.30 ± 0.22
	18.3 - 22.4	8.9 - 12.6	11.2 - 16.1	4.4 - 6.1	1.5 - 2.7	1.7 - 3.1
Berekhat HaMeshoshim	20.15 ± 2.02	10.10 ± 1.06	11.85 ± 1.53	4.68 ± 0.70	2.03 ± 0.35	2.16 ± 0.38
	16.9 - 23.2	8.3 - 11.8	8.5 - 14.4	3.3 - 5.8	1.5 - 2.7	1.5 - 2.6
Yehudiya	16.58 ± 3.99	8.24 ± 1.66	9.87 ± 2.14	3.4 ± 0.78	1.92 ± 0.53	1.96 ± 0.59
	10.3 - 23.2	5.5 - 11.4	6.4 - 13.9	2.8 - 5.5	1.1 - 3.0	0.9 - 3.3
Nahal Meshoshim	23.69 ± 1.37	11.7 ± 0.93	13.87 ± 0.92	5.12 ± 0.38	2.51 ± 0.39	2.73 ± 0.28
	21.4 - 26.0	10.0 - 13.5	12.1 - 16.0	4.5 - 5.8	1.6 - 3.0	2.2 - 3.3
Nahal Tavor	12.99 ± 3.28	6.64 ± 1.65	8.15 ± 2.07	3.07 ± 0.71	1.41 ± 0.36	1.55 ± 0.46
	10.6 - 22.5	5.2 - 11.3	6.6 - 14.1	2.3 - 5.3	1.1 - 2.4	0.9 - 2.9
Enot Huga	19.67 ± 1.97	9.99 ± 1.03	11.8 ± 1.17	4.82 ± 0.55	2.22 ± 0.27	2.66 ± 0.33
	16.1 - 23.1	7.7 - 11.9	9.1 - 13.4	3.7 - 5.7	1.8 - 2.7	2.0 - 3.2
Gan Hashelosha	16.32 ± 1.66	8.9 ± 0.85	10.0 ± 0.90	4.03 ± 0.40	2.00 ± 0.26	2.21 ± 0.33
	14.0 - 20.2	6.7 - 10.1	8.2 - 11.6	3.3 - 5.5	1.5 - 2.4	2.5 - 3.0
En Hanaziv	19.19 ± 2.88	9.58 ± 1.30	11.59 ± 1.57	4.52 ± 0.66	2.16 ± 0.30	2.59 ± 0.39
	12.0 - 22.4	6.1 - 11.3	7.6 - 13.4	3.0 - 5.5	1.5 - 2.7	1.7 - 3.2
En Parta	21.72 ± 1.15	10.72 ± 0.73	13.45 ± 0.83	5.32 ± 0.38	2.02 ± 0.29	2.34 ± 0.31
	20.1 - 24.0	9.5 - 12.4	12.4 - 15.4	4.5 - 6.1	1.38 - 2.7	1.7 - 3.0

RATIOS

	SD / SH	MH / SH	MD / MH	MH / SD	NW / NDe	NW / MD	NDe / MD
Nahal Dan	0.48 ± 0.02	0.54 ± 0.03	0.43 ± 0.03	1.13 ± 0.07	1.12 ± 0.10	0.52 ± 0.05	0.47 ± 0.07
	0.49 - 0.51	0.48 - 0.59	0.38 - 0.48	0.97 - 0.27	0.97 - 1.33	0.43 - 0.62	0.34 - 0.63
Nahal Senir	0.49 ± 0.02	0.58 ± 0.02	0.41 ± 0.01	1.17 ± 0.04	0.91 ± 0.08	0.48 ± 0.05	0.53 ± 0.06
	0.46 - 0.52	0.55 - 0.62	0.39 - 0.44	1.10 - 1.23	0.77 - 1.06	0.37 - 0.56	0.44 - 0.67
Bet Hillel N	0.50 ± 0.02	0.58 ± 0.03	0.42 ± 0.02	1.17 ± 0.03	0.92 ± 0.09	0.46 ±v 0.06	0.50 ± 0.05
	0.45 - 0.54	0.52 - 0.63	0.38 - 0.44	1.10 - 1.22	0.71 - 1.06	0.35 - 0.60	0.43 - 0.63
Nahal Gilbon	0.50 ± 0.02	0.62 ± 0.03	0.40 ± 0.02	1.23 ± 0.06	0.89 ± 0.10	0.40 ± 0.06	0.45 ± 0.05
	0.48 - 0.54	0.58 - 0.68	0.35 - 0.45	1.11 - 1.33	0.68 - 1.05	0.30 - 0.53	0.35 - 0.57
Berekhat HaMeshoshim	0.50 ± 0.03	0.59 ± 0.05	0.39 ± 0.02	1.17 ± 0.07	0.94 ± 0.06	0.44 ± 0.06	0.47 ± 0.07
	0.51 - 0.53	0.49 - 0.66	0.33 - 0.42	1.03 - 1.28	0.82 - 1.03	0.33 - 0.56	0.34 - 0.60
Yehudiya	0.50 ± 0.03	0.60 ± 0.04	0.39 ± 0.03	1.20 ± 0.08	0.99 ± 0.09	0.50 ± 0.09	0.51 ± 0.09
	0.51 - 0.56	0.49 - 0.65	0.35 - 0.45	0.99 - 1.33	0.87 - 1.20	0.35 - 0.68	0.29 - 0.75
Nahal Meshoshim	0.49 ± 0.03	0.59 ± 0.03	0.37 ± 0.02	1.19 ± 0.06	0.92 ± 0.12	0.49 ± 0.09	0.54 ± 0.07
	0.45 - 0.53	0.53 - 0.64	0.33 - 0.42	1.09 - 1.27	0.60 - 1.14	0.34 - 0.65	0.42 - 0.72
Nahal Tavor	0.51 ± 0.02	0.63 ± 0.03	0.38 ± 0.03	1.23 ± 0.05	0.93 ± 0.09	0.46 ± 0.05	0.50 ± 0.07
	0.52 - 0.55	0.57 - 0.67	0.33 - 0.45	1.12 - 1.24	0.79 - 1.20	0.39 - 0.57	0.38 - 0.63
Enot Huga	0.51 ± 0.02	0.60 ± 0.02	0.41 ± 0.02	1.18 ± 0.03	0.84 ± 0.06	0.46 + 0.04	0.55 + 0.05
	0.52 - 0.54	0.56 - 0.63	0.36 - 0.45	1.12 - 1.24	0.69 - 0.93	0.40 - 0.56	0.46 - 0.67
Gan Hashelosha	0.50 ± 0.02	0.62 ± 0.03	0.40 ± 0.02	1.24 ± 0.07	0.91 ± 0.05	0.50 ± 0.05	0.55 ± 0.07
	0.51 - 0.54	0.55 - 0.65	0.37 - 0.43	1.13 - 1.33	0.80 - 1.00	0.38 - 0.57	0.41 - 0.71
En Hanaziv	0.50 ± 0.02	0.61 ± 0.03	0.39 ± 0.01	1.21 ± 0.04	0.84 ± 0.05	0.48 ± 0.04	0.57 ± 0.04
	0.51 - 0.53	0.62 - 0.65	0.40 - 0.41	1.15 - 1.30	0.76 - 0.93	0.40 - 0.54	0.49 - 0.63
En Parta	0.49 ± 0.02	0.63 ± 0.02	0.40 ± 0.02	1.26 ± 0.05	0.87 ± 0.10	0.38 ± 0.05	0.44 ± 0.06
	0.46 - 0.55	0.57 - 0.65	0.35 - 0.43	1.14 - 1.36	0.72 - 1.07	0.27 - 0.50	0.29 - 0.55

Appendix 1 B. Measurements (mm), rib characters and ratios of the seven samples of *M. costata costata* (mean ± S.D., and observed range).

MEASUREMENTS (mm) AND RIB CHARACTERS

	Shell Height	Shell Diameter	Mouth Height	Mouth Diameter	Notch Width	Notch Depth	No of ribs	Rib Form	Rib Length
Bet Hillel S	18.0 ± 1.80 15.6 - 22.7	8.59 ± 0.82 7.4 - 10.4	9.70 ± 0.90 8.6 - 12.0	4.17 ± 0.48 3.4 - 5.0	2.09 ± 0.34 1.6 - 3.0	2.33 ± 0.35 1.9 - 3.4	11.5 ± 1.2 10 - 14	1.8 ± 0.4 1 - 2	3.4 ± 0.4 3 - 4
Sede Nehemya	18.70 ± 1.23 17.9 - 21.2	8.77 ± 0.58 7.5 - 9.9	10.15 ± 0.70 9.3 - 11.4	4.38 ± 0.32 3.8 - 5.2	2.37 ± 0.23 1.8 - 2.7	2.59 ± 0.28 2.0 - 3.0	11.5 ± 1.0 10 - 13	1.8 ± 0.4 1 - 2	3.6 ± 0.4 3 - 4
Lahavot	22.00 ± 1.06 20.4 - 23.4	10.31 ± 0.62 9.2 - 11.9	12.4 ± 0.70 10.6 - 13.4	5.8 ± 0.28 4.7 - 5.6	2.64 ± 0.39 2.1 - 3.9	2.9 ± 0.38 2.2 - 3.9	10.6 ± 0.8 9 - 12	2.1 ± 0.3 2 - 3	3.6 ± 0.3 3 - 4
Eastern Canal	15.69 ± 1.24 14.1 - 17.8	7.49 ± 0.71 6.5 - 8.9	8.42 ± 0.66 7.6 - 9.7	3.72 ± 0.35 3.1 - 4.4	2.6 ± 0.24 1.7 - 2.4	2.30 ± 0.25 1.8 - 2.8	10.6 ± 1.0 9 - 12	1.6 ± 0.5 1 - 2	3.6 ± 0.4 3 - 4
Benot Ya'aqov	14.95 ± 2.26 12.2 - 21.9	7.20 ± 0.82 5.9 - 9.2	8.44 ± 1.11 6.9 - 11.9	3.65 ± 0.43 3.1 - 4.8	2.01 ± 0.29 1.5 - 2.4	2.08 ± 0.25 1.7 - 2.5	11.4 ± 1.4 9 - 14	1.8 ± 0.4 1 - 2	3.4 ± 0.5 3 - 4
En Yezer	22.18 ± 1.75 20.0 - 26.7	10.41 ± 0.91 8.7 - 12.3	11.36 ± 0.94 10.3 - 14.0	5.01 ± 0.33 4.5 - 5.7	2.49 ± 0.23 2.1 - 3.0	2.93 ± 0.33 2.16 - 3.6	11.3 ± 1.1 9 - 13	1.7 ± 0.5 1 - 2	3.7 ± 0.5 3 - 4
Jordan Inlet	24.60 ± 2.09 16.2 - 23.8	11.43 ± 0.90 8.0 - 10.7	12.95 ± 0.97 11.0 - 15.3	5.68 ± 0.42 4.9 - 6.8	2.84 ± 0.36 2.2 - 3.3	3.09 ± 0.35 2.1 - 3.7	10.9 ± 1.1 9 - 13	1.8 ± 0.4 1 - 2	3.6 ± 0.5 3 - 4

RATIOS

	SD / SH	MH / SH	MD / MH	MH / SD	NW / NDe	NW / MD	NDe / MD	Rib Index
Bet Hillel S	0.48 ± 0.02 0.45 - 0.51	0.54 ± 0.02 0.50 - 0.58	0.44 ± 0.03 0.38 - 0.50	1.13 ± 0.03 1.04 - 1.17	0.90 ± 0.06 0.77 - 1.00	0.50 ± 0.06 0.39 - 0.60	0.55 ± 0.06 0.44 - 0.68	4.21 ± 0.50 3.43 - 5.00
Sede Nehemya	0.47 ± 0.02 0.44 - 0.49	0.54 ± 0.02 0.50 - 0.60	0.43 ± 0.02 0.40 - 0.46	1.16 ± 0.05 1.10 - 1.26	0.92 ± 0.07 0.83 - 1.05	0.54 ± 0.06 0.43 - 0.63	0.59 ± 0.07 0.47 - 0.73	4.13 ± 0.43 3.38 - 4.90
Lahavot	0.47 ± 0.03 0.44 - 0.56	0.55 ± 0.03 0.51 - 0.63	0.42 ± 0.01 0.40 - 0.45	1.17 ± 0.04 1.09 - 1.27	0.91 ± 0.07 0.80 - 1.00	0.52 ± 0.08 0.39 - 0.76	0.57 ± 0.07 0.46 - 0.76	4.48 ± 0.50 3.67 - 5.60
Eastern Canal	0.48 ± 0.03 0.43 - 0.52	0.54 ± 0.03 0.47 - 0.60	0.44 ± 0.02 0.39 - 0.49	1.13 ± 0.06 1.01 - 1.21	0.90 ± 0.04 0.81 - 1.06	0.56 ± 0.06 0.43 - 0.70	0.62 ± 0.06 0.45 - 0.73	4.54 ± 0.45 3.75 - 5.44
Benot Ya'aqov	0.48 ± 0.02 0.49 - 0.52	0.57 ± 0.02 0.52 - 0.61	0.43 ± 0.02 0.40 - 0.46	1.17 ± 0.04 1.09 - 1.26	0.97 ± 0.07 0.83 - 1.08	0.55 ± 0.06 0.44 - 0.67	0.57 ± 0.06 0.42 - 0.71	4.34 ± 0.66 3.29 - 5.56
En Yezer	0.47 ± 0.02 0.43 - 0.52	0.51 ± 0.03 0.47 - 0.59	0.44 ± 0.02 0.41 - 0.48	1.12 ± 0.06 1.03 - 1.30	0.85 ± 0.02 0.76 - 1.11	0.50 ± 0.05 0.42 - 0.59	0.58 ± 0.07 0.48 - 0.74	4.22 ± 0.46 3.46 - 5.22
Jordan Inlet	0.48 ± 0.02 0.49 - 0.51	0.54 ± 0.03 0.49 - 0.62	0.44 ± 0.03 0.39 - 0.52	1.13 ± 0.05 1.04 - 1.27	0.92 ± 0.07 0.80 - 1.06	0.50 ± 0.05 0.43 - 0.58	0.54 ± 0.05 0.40 - 0.65	4.41 ± 0.52 3.54 - 5.44

Appendix 1 C. Measurements (mm), rib characters and ratios of the six samples of *M. costata jordanica* (mean ± S.D., and observed range).

MEASUREMENTS (mm) and RIB CHARACTERS

	Shell Height	Shell Diameter	Mouth Height	Mouth Diameter	Notch Width	Notch Depth	No of ribs	Rib Form	Rib Length
En Sheva	11.56 ± 1.67 13.1 - 19.8	8.49 ± 0.93 6.9 - 10.4	8.66 ± 0.94 7.0 - 10.6	4.12 ± 0.48 3.4 - 5.1	11.10 ± 0.32 1.6 - 2.7	2.15 ± 0.30 1.7 - 2.8	10.9 ± 1.1 10 - 14	1.8 ± 0.4 1 - 2	3.9 ± 0.3 3 - 4
Ginnosar	16.84 ± 1.15 15.1 - 19.3	8.70 ± 0.49 7.7 - 9.5	9.11 ± 0.46 8.2 - 10.1	4.13 ± 0.36 3.4 - 4.7	11.21 ± 0.45 1.6 - 2.2	2.40 ± 0.44 11.6 - 3.4	10.0 ± 0.9 9 - 12	1.3 ± 0.5 1 - 2	3.9 ± 0.3 3 - 4
En Raqqat	18.2 ± 1.73 14.4 - 20.6	9.90 ± 0.76 8.1 - 11.0	9.74 ± 0.81 8.1 - 11.4	4.47 ± 0.40 3.6 - 5.0	2.22 ± 0.38 1.4 - 3.0	2.54 ± 0.37 1.8 - 3.3	11.3 ± 1.0 10 - 14	1.8 ± 0.3 1 - 2	3.8 ± 0.3 3 - 4
En Gev	13.64 ± 1.40 12.3 - 17.8	7.94 ± 0.61 7.2 - 9.7	8.20 ± 0.88 6.5 - 10.3	3.76 ± 0.31 3.4 - 4.5	1.96 ± 0.17 1.8 - 2.4	2.20 ± 0.23 11.9 - 3.0	10.7 ± 1.0 9 - 13	1.6 ± 0.5 1 - 2	3.5 ± 0.3 3 - 4
Haon	11.5 ± 1.05 12.9 - 16.8	7.43 ± 0.46 6.7 - 8.3	7.98 ± 0.55 6.9 - 8.9	3.60 ± 0.22 3.3 - 4.1	1.86 ± 0.22 1.5 - 2.4	2.10 ± 0.27 1.6 - 2.8	10.4 ± 1.1 8 - 13	1.6 ± 0.5 1 - 2	3.6 ± 0.4 3 - 4
Bet Gavriel	14.17 ± 1.13 11.9 - 16.3	7.39 ± 0.59 6.3 - 8.4	7.78 ± 0.58 6.5 - 8.8	3.36 ± 0.29 2.9 - 3.9	1.82 ± 0.54 1.3 - 2.2	2.7 ± 0.22 1.7 - 2.4	11.9 ± 1.3 9 - 14	1.6 ± 0.4 1 - 2	3.8 ± 0.3 3 - 4

RATIOS

	SD / SH	MH / SH	MD / MH	MH / SD	NW / NDe	NW / MD	NDe / MD	Rib Index
En Sheva	0.55 ± 0.03 0.51 - 0.61	0.56 ± 0.03 0.49 - 0.62	0.48 ± 0.02 0.43 - 0.51	1.02 ± 0.06 0.96 - 1.10	0.98 ± 0.06 0.85 - 1.07	0.51 ± 0.08 0.38 - 0.78	0.53 ± 0.08 0.38 - 0.73	5.08 ± 0.51 3.9 - 5.9
Ginnosar	0.52 ± 0.03 0.48 - 0.57	0.56 ± 0.05 0.46 - 0.66	0.44 ± 0.02 0.41 - 0.48	1.07 ± 0.10 0.92 - 1.34	0.92 ± 0.08 0.79 - 0.97	0.54 ± 0.12 0.35 - 0.64	0.59 ± 0.11 0.37 - 0.80	5.28 ± 0.46 4.1 - 6.1
En Raqqat	0.54 ± 0.02 0.52 - 0.61	0.54 ± 0.03 0.48 - 0.61	0.46 ± 0.02 0.48 - 0.61	0.98 ± 0.04 0.90 - 1.06	0.87 ± 0.07 0.77 - 1.05	0.50 ± 0.06 0.38 - 0.67	0.57 ± 0.07 0.48 - 0.73	4.86 ± 0.42 3.9 - 5.6
En Gev	0.58 ± 0.03 0.55 - 0.63	0.59 ± 0.03 0.53 - 0.62	0.47 ± 0.03 0.43 - 0.54	1.01 ± 0.04 0.91 - 1.10	0.89 ± 0.06 0.79 - 0.97	0.52 ± 0.04 0.41 - 0.59	0.59 ± 0.04 0.52 - 0.67	5.49 ± 0.47 4.8 - 6.3
Haon	0.53 ± 0.03 0.48 - 0.58	0.57 ± 0.03 0.50 - 0.63	0.45 ± 0.02 0.39 - 0.49	1.07 ± 0.04 0.02 - 1.17	0.89 ± 0.07 0.73 - 1.00	0.52 ± 0.04 0.43 - 0.59	0.58 ± 0.05 0.49 - 0.68	5.16 ± 0.59 4.2 - 6.6
Bet Gavriel	0.52 ± 0.03 0.49 - 0.57	0.55 ± 0.02 0.51 - 0.59	0.43 ± 0.02 0.40 - 0.47	1.05 ± 0.04 0.99 - 1.14	0.88 ± 0.085 0.73 - 1.05	0.54 ± 0.06 0.41 - 0.67	0.62 ± 0.06 0.54 - 0.77	4.43 ± 0.48 3.6 - 5.7

Appendix 1 D. Measurements, rib characters and ratios of the three intermediate samples (mean ± S.D., and observed range).

MEASUREMENTS (mm) and RIB CHARACTERS

	Shell Height	Shell Diameter	Mouth Height	Mouth Diameter	Notch Width	Notch Depth	No of ribs	Rib Form	Rib Length
c. jordanica - c. costata Meshoshim Outlet	19.83 ± 1.92 16.2 - 23.8	9.68 ± 0.76 8.0 - 10.7	10.46 ± 1.11 8.6 - 12.3	4.74 ± 0.39 4.2 - 5.4	2.47 ± 0.43 1.8 - 3.6	2.79 ± 0.42 2.0 - 3.8	10.1 ± 0.9 9 - 13	16.2 ± 0.4 1 - 2	3.65 ± 0.33 3 - 4
c. jordanica - c. costata Kinneret 208	19.53 ± 2.41 16.9 - 25.8	9.63 ± 0.95 8.1 - 11.8	10.19 ± 1.10 8.9 - 13.0	4.73 ± 0.63 3.8 - 6.5	2.48 ± 0.54 1.6 - 4.8	2.80 ± 0.53 2.0 - 3.8	10.0 ± 0.9 9 - 12	1.3 ± 0.47 1 - 2	3.6 ± 0.3 3 - 4
buccinoidea - saulcyi En Malkoah	20.90 ± 1.23 19.3 - 22.9	9.59 ± 1.23 7.9 - 11.3	10.82 ± 0.29 8.5 - 12.8	4.45 ± 0.50 3.7 - 5.4	2.15 ± 0.27 1.8 - 2.7	2.64 ± 0.31 2.2 - 3.4			

RATIOS

	SD / SH	MH / SH	MD / MH	MH / SD	NW / NDe	NW / MD	NDe / MD	Rib Index
c. jordanica - c. costata Meshoshim Outlet	0.49 ± 0.03 0.43 - 0.53	0.53 ± 0.03 0.47 - 0.57	0.46 ± 0.04 0.40 - 0.52	1.08 ± 0.07 0.96 - 1.23	0.89 ± 0.05 0.78 - 0.98	0.52 ± 0.08 0.42 - 0.73	0.54 ± 0.08 0.47 - 0.77	4.88 ± 0.58 4.27 - 6.38
c. jordanica - c. costata Kinneret 208	0.49 ± 0.03 0.46 - 0.56	0.52 ± 0.03 0.48 - 0.62	0.46 ± 0.04 0.39 - 0.55	1.06 ± 0.06 0.94 - 1.17	0.88 ± 0.05 0.81 - 1.00	0.52 ± 0.08 0.38 - 0.67	0.59 ± 0.08 0.47 - 0.80	4.98 ± 0.43 3.83 - 5.84
buccinoidea - saulcyi En Malkoah	0.46 ± 0.03 0.40 - 0.50	0.52 ± 0.05 0.43 - 0.59	0.41 ± 0.03 0.36 - 0.45	1.13 ± 0.05 1.05 - 1.26	0.81 ± 0.05 0.74 - 0.90	0.49 ± 0.07 0.38 - 0.61	0.60 ± 0.06 0.48 - 0.70	

Appendix 1 E. Measurements (mm), rib characters and ratios of the eight samples of *M. saulcyi* (mean ± S.D., and observed range).

MEASUREMENTS (mm) AND RIB CHARACTERS

	Shell height	Shell diameter	Mouth height	Mouth diameter	Notch width	Notch depth	No of ribs	Rib Form	Rib Length
Hammat Gader	14.71 ± 1.33 13.0 - 18.4	7.09 ± 0.73 6.0 - 9.5	7.79 ± 0.83 6.7 - 9.5	3.31 ± 0.33 2.9 - 4.2	1.50 ± 0.19 1.2 - 2.1	1.90 ± 0.14 1.6 - 2.2	12.8 ± 0.83 12 - 15	2.8 ± 0.5 2 - 4	2.8 ± 0.5 2 - 3.5
Ma'ayan Harod	14.22 ± 1.20 12.7 - 17.1	6.70 ± 0.65 6.0 - 8.0	7.66 ± 0.42 7.0 - 8.4	3.42 ± 0.30 2.9 - 4.0	1.43 ± 0.17 1.1 - 1.8	1.72 ± 0.21 1.4 - 2.1	12.7 ± 1.5 10 - 15	2.2 ± 0.7 1 - 3	2.9 ± 0.7 2 - 4
Enot Huga	17.18 ± 1.16 15.4 - 20.5	8.7 ± 0.65 7.1 - 9.3	8.97 ± 0.71 7.7 - 10.6	4.06 ± 0.33 3.6 - 4.7	1.64 ± 0.16 1.3 - 1.9	1.97 ± 0.19 1.7 - 2.9	13.0 ± 1.3 11 - 17	2.2 ± 0.4 2 - 3	2.1 ± 0.2 2 - 2.5
Gan HaShelosha	14.59 ± 1.27 13.2 - 17.3	6.69 ± 0.49 5.9 - 7.8	7.50 ± 0.50 6.8 - 8.5	3.41 ± 0.26 3.1 - 3.9	1.40 ± 0.20 0.9 - 1.8	1.88 ± 0.22 1.4 - 2.4	12.8 ± 1.6 10 - 15	3.0 ± 0.3 2 - 4	3.3 ± 0.6 2 - 4
Sheluhot	15.43 ± 0.81 14.6 - 17.4	6.58 ± 0.56 5.8 - 8.1	7.42 ± 0.56 6.8 - 8.7	3.36 ± 0.27 3.0 - 4.2	1.40 ± 0.17 1.1 - 1.8	1.77 ± 0.19 1.6 - 2.2	10.8 ± 1.2 9 - 14	3.7 ± 0.6 2 - 4	3.9 ± 0.4 3 - 4
En HaNaziv	16.89 ± 1.57 13.1 - 19.3	7.14 ± 0.45 5.9 - 8.0	8.27 ± 0.55 7.1 - 9.2	3.58 ± 0.30 2.9 - 4.0	1.52 ± 0.15 1.3 - 1.8	1.91 ± 0.20 1.4 - 2.3	12.6 ± 1.0 11 - 14	3.1 ± 0.5 2 - 4	2.8 ± 0.4 2 - 3
Sede Eliyyahu	14.80 ± 1.05 13.6 - 18.0	6.31 ± 0.42 5.6 - 7.0	7.18 ± 0.57 5.9 - 8.1	3.32 ± 0.24 2.8 - 3.6	1.54 ± 0.18 1.2 - 1.8	1.81 ± 0.19 1.4 - 2.1	13.4 ± 1.4 10 - 16	2.9 ± 0.5 2 - 4	2.6 ± 0.5 2 - 3
En Hamma	19.93 ± 2.34 17.5 - 26.0	8.58 ± 1.05 6.9 - 10.5	9.58 ± 0.94 8.6 - 0.9	4.18 ± 0.43 3.5 - 5.2	1.64 ± 0.26 1.2 - 2.1	1.95 ± 0.20 1.5 - 2.4	13.8 ± 1.7 11 - 16	2.1 ± 0.6 1 - 3	3.1 ± 0.2 3 - 3.5

RATIOS

	SD / SH	MH / SH	MD / MH	MH / SD	NW / NDe	NW / MD	NDe / MD	Rib Index
Hammat Gader	0.48 ± 0.02 0.45 - 0.51	0.53 ± 0.02 0.50 - 0.58	0.43 ± 0.02 0.38 - 0.46	1.10 ± 0.05 1.00 - 1.22	0.79 ± 0.06 0.69 - 0.95	0.45 ± 0.05 0.33 - 0.55	0.57 ± 0.05 0.44 - 0.64	3.77 ± 0.24 3.29 - 4.17
Ma'ayan Harod	0.47 ± 0.02 0.42 - 0.51	0.54 ± 0.03 0.49 - 0.60	0.45 ± 0.03 0.37 - 0.49	1.15 ± 0.08 1.02 - 1.33	0.83 ± 0.07 0.71 - 0.96	0.42 ± 0.06 0.35 - 0.60	0.51 ± 0.06 0.40 - 0.70	3.77 ± 0.50 3.00 - 4.90
Enot Huga	0.47 ± 0.02 0.44 - 0.52	0.52 ± 0.02 0.47 - 0.57	0.45 ± 0.02 0.42 - 0.50	1.11 ± 0.04 1.04 - 1.17	0.83 ± 0.06 0.71 - 0.94	0.40 ± 0.04 0.35 - 0.50	0.49 ± 0.04 0.40 - 0.59	3.73 ± 0.43 2.65 - 4.25
Gan HaShelosha	0.46 ± 0.03 0.40 - 0.51	0.51 ± 0.03 0.45 - 0.55	0.45 ± 0.03 0.41 - 0.51	1.12 ± 0.07 0.98 - 1.22	0.75 ± 0.10 0.50 - 0.89	0.41 ± 0.07 0.27 - 0.57	0.56 ± 0.06 0.45 - 0.67	3.65 ± 0.43 2.87 - 4.45
Sheluhot	0.43 ± 0.03 0.37 - 0.48	0.48 ± 0.03 0.43 - 0.58	0.45 ± 0.03 0.41 - 0.50	1.13 ± 0.07 1.03 - 1.26	0.79 ± 0.09 0.64 - 1.00	0.42 ± 0.06 0.29 - 0.50	0.53 ± 0.06 0.36 - 0.61	3.93 ± 0.51 2.93 - 5.00
En Hanaziv	0.42 ± 0.02 0.39 - 0.46	0.49 ± 0.04 0.44 - 0.54	0.43 ± 0.03 0.37 - 0.50	1.16 ± 0.07 1.01 - 1.26	0.80 ± 0.06 0.68 - 0.92	0.43 ± 0.05 0.34 - 0.54	0.54 ± 0.06 0.42 - 0.62	3.38 ± 0.28 2.86 - 3.82
Sede Eliyyahu	0.43 ± 0.02 0.38 - 0.47	0.48 ± 0.03 0.40 - 0.54	0.46 ± 0.02 0.42 - 0.49	1.14 ± 0.06 1.02 - 1.28	0.85 ± 0.05 0.79 - 0.97	0.46 ± 0.05 0.36 - 0.55	0.54 ± 0.04 0.44 - 0.61	3.35 ± 0.40 2.50 - 4.30
En Hamma	0.42 ± 0.03 0.38 - 0.48	0.48 ± 0.04 0.38 - 0.59	0.44 ± 0.03 0.37 - 0.49	1.14 ± 0.09 0.86 - 1.28	0.84 ± 0.10 0.62 - 1.00	0.40 ± 0.08 0.24 - 0.57	0.47 ± 0.07 0.36 - 0.66	3.28 ± 0.43 2.50 - 4.18

THE GENUS *VOLVARINA* (GASTROPODA: MARGINELLIDAE) IN THE CAPE VERDE ISLANDS

D. MORENO[1] & L.P. BURNAY[2]

Abstract   Species of the genus Volvarina *from the Cape Verde Islands are reviewed. Nine species are recognized, of which seven have already been described:* Volvarina taeniata *(Sowerby, 1846),* V. verdensis *(E.A. Smith, 1875),* V. mediocincta *(E.A. Smith, 1875),* V. corallina *(Bavay, 1910)* V. cernita *(Locard, 1897),* V. sauliae *(Sowerby, 1846) and* V. joubini *(Dautzenberg & Fischer, 1906). Two new species are described:* V. boyeri *n. sp. and* V. nuriae *n. sp. Lectotypes are designated for* V. taeniata, V. verdensis *and* V. mediocincta *and a neotype for* V. sauliae. *The name* Volvarina obscura *(Reeve, 1865), refers to a species from the Red Sea and Gulf of Aden, very similar to the* Volvarina *complex from the Cape Verde Islands.*

Key words   Taxonomy, Cape Verde Islands, Red Sea, polymorphism, endemism.

INTRODUCTION

The genus *Volvarina* belongs to the family Marginellidae, one of the most conspicuous among the prosobranch gastropods of West Africa. This genus is well represented in the Cape Verde Archipelago where at least 9 species, all endemic, live. The archipelago's 10 islands and several islets are some 500 km away from mainland West Africa, i.e. far enough for the fauna to be considerably isolated. It is an ideal setting to study the processes of speciation and related topics such as species' capacity for dispersal and the resulting geographical distributions of the species.

The molluscan fauna of the Cape Verde Islands has been studied by many authors, including Jousseaume (1875, 1877, 1881), Rochebrune (1881a, b), Locard (1897-98), Dautzenberg (1910), Dautzenberg & Fischer (1906), Knudsen (1956), Marche-Marchad (1956), Burnay and Monteiro (1977), Cosel (1982a, b, c), and Fernandes (1987). There are 21 species names for *Volvarina* listed in the literature, either described with a type locality in the Cape Verde Islands or cited for the archipelago. All are based only on conchological characters, and in need of revision. The shell of these marginellids is small, smooth, with a paucispiral protoconch and quite a variable pigmentation of spiral bands. These characters are of limited use for distinguishing species and are most useful at genus level. The radula, where present, is useful for separating genera (Coan, 1965; Coovert & Coovert, 1995), and often helpful for defining species groups (Coovert & Coovert, 1990).

Animal coloration is very useful at species level (Coovert & Coovert, 1995). The pigmentation patterns of the head-foot and mantle in the living animals are usually bright and have been shown to be stable and extremely informative for separating closely related species (Gofas & Fernandes, 1988, 1992; Gofas, 1989), and will be given particular attention in this paper.

ABBREVIATIONS USED

[1] c/Araña, apartmentos Las Dumas 2, 04150-Cabo de Gato, Almería, Spain.
[2] Quinta do Vale Viado, Povoa de Cima, 2640-Mafra, Portugal.

BMNH The Natural History Museum, London.
MOM Muséum Océanographique de Monaco.
RMNH Nationaal Natuurhistorische Museum, Leiden.
MNCN Museo Nacional de Ciencias Naturales, Madrid.
ER Private collection of Emilio Rolán (Vigo, Spain).
FF Private collection of the late Francisco Fernandes.
FB Private collection of Franck Boyer (Sevran, France).
DM Private collection of Diego Moreno (Cabo de Gata, Spain).
EM2 Expedición Macaronesia 2 (July 1977), of the proyect "Evaluación de los recursos naturales litorales de la República de Cabo Verde" (Conserjería Territorial de Medio Ambiente del Gobierno de Canarias).
sp live specimens
sh shells
fg fragments

Material examined

Most of the material examined (UAM collection) was collected during the PEICV expedition to the Cape Verde Islands, in which both authors took part (August, 1985). Most of the data on colour patterns of living animals were taken on that occasion. Other material studied was collected by L.P. Burnay in 1975-1976 (IIT) and 1978–79, by R. von Cosel in 1978–79 (MNHN), by E. Rolán in 1978–79, 1980, 1981, 1986, 1987, 1988 (ER) and 1997 (EM2), and by the "Tydeman" expedition in 1982 (RMNH). We also examined specimens from the collection of the late Francisco Fernandes (FF), and part of the type material of *V. boyeri* in F. Boyer's collection (FB). We obtained material from all the major islands and some islets, studying 47 different localities (Map 1).

We examined type specimens in the following institutions: types of Locard, Jousseaume, and Bavay in MNHN; Sowerby, E.A. Smith, and Reeve in BMNH; and Dautzenberg & Fischer in MOM.

For the older museum material, some labels indicate only the name of an island, but others (including most types) only state "Cape Verde Archipelago" or even "Cape Verde", which may be confused with the mainland Cap Vert (the peninsula around Dakar, Senegal). Some of the type material examined (e.g. *V. taeniata* and *V. sauliae)* was described as being of unknown origin.

From MNHN, we also examined five lots from the Red Sea, Obock (Djibouti) and Aden, with large numbers of a *Volvarina* species extremely similar to the Cape Verde species, and originally labelled as *Marginella taeniata* Sow.

Methods

Clarifying the complex taxonomic problems in the genus was mainly based on observing pigmentation patterns of live animals, and thus required collecting and sorting the animals while alive. To do so, specimens were hand-picked while scuba-diving or snorkeling at depths of 1-18 m during the PEICV. Most specimens were collected at 1-2 m on rocky bottoms with coral slabs, always surrounded by sand. Some dredging attempts were made at various depths with very poor results.

The live animals were observed under a stereomicroscope, and coloured drawings prepared to take note of the pigmentation patterns and tones. In some cases, colour slides were also taken.
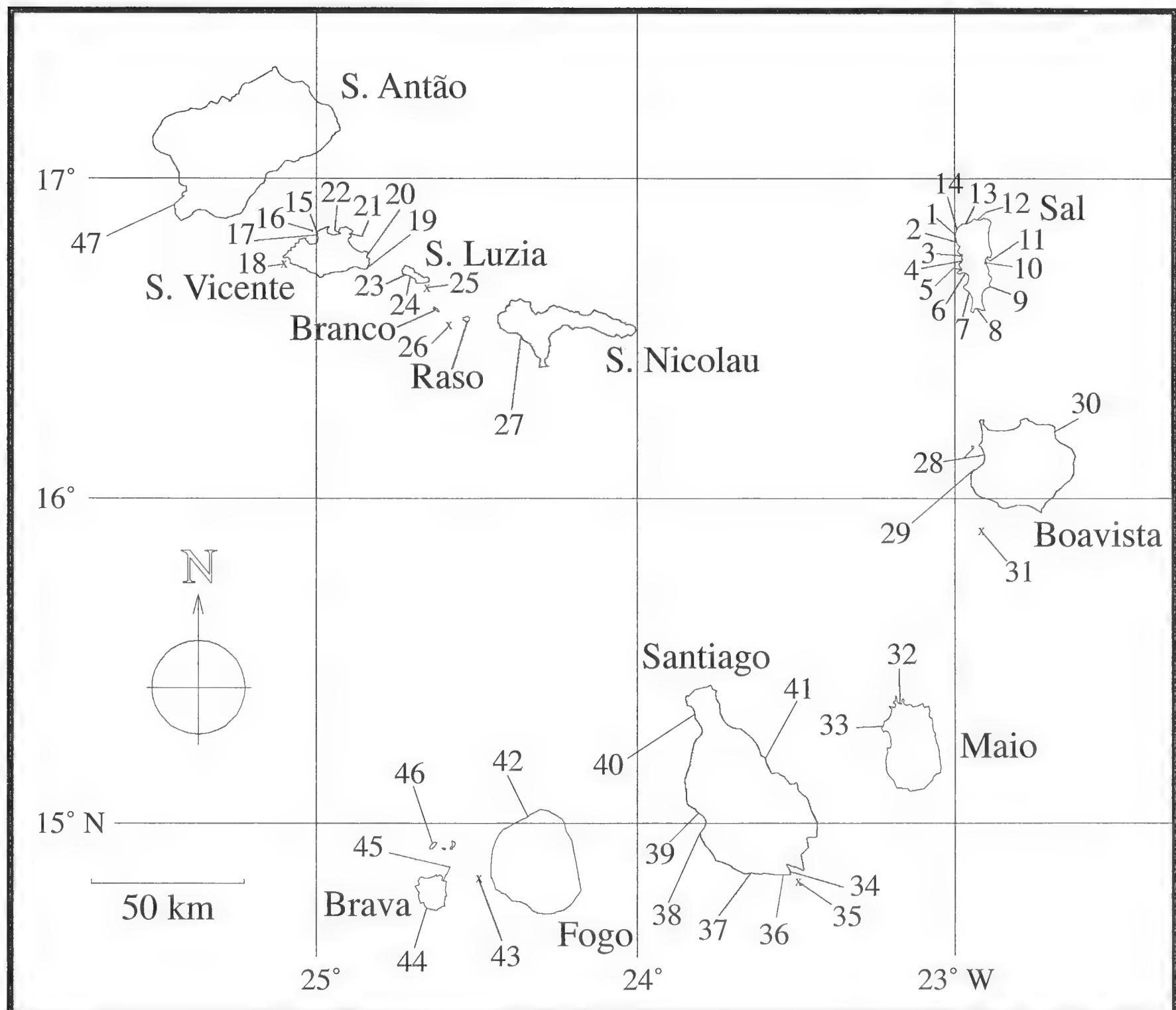
Map 1 Cape Verde archipelago and collection localities (origin of the samples in brackets). **Sal: 1** *Ponta Preta*, 16°50′N, 23°00′W (PEICV). **2** *Rigona*, 16°47′N, 23°00′W (PEICV). **3** *Baia Palmeira*, 16°45′N, 22°59′W (PEICV, MNHN and FF). **4** *Baia Fontona*, 16°44′N, 22°59′ W (MNHN and FB). **5** *Joaquim Petinha*, 16°43′N, 22°59′W. (PEICV). **6** *Baia Mordeira*, 16°40′N, 22°57′W (PEICV) and (MNHN). **7** *Baia Algodoeiro*, 16°38′N, 22°57′W (MNHN). **8** *S. Maria*, 16°36′N, 22°55′W (PEICV). **9** *Ponta Fragata*, 16°39′N, 22°53′W (MNHN). **10** *Parda*, 16°44′N, 22°54′W (PEICV, MNHN and ER). **11** *Ponta de Pedra Lume*, 16°45′N, 22°53′W (ER). **12** *Guincho do Ninho*, 16°53′N, 22°55′W (PEICV). **13** *Palhona*, 16°52′N, 22°57′W (PEICV). **14** *Ponta de Leste and Pesqueiro do Aire*, 16°51′N, 23°00′W (PEICV, ER and FF). **S. Vicente: 15** *Ninho do Guincho*, 16°54′N, 25°00′W (PEICV). **16** *Ilhéu dos Passaros*, 16°54′N, 25°01′W (−18 m scuba, PEICV). **17** *Matiota, Porto Mindelo*, 16°54′N, 25°00′W (PEICV and FF). **18** 16°48′N, 25°06′W (−45 m dredging, CANCAP–VI Sta. 6.146, RMNH). **19** *Saragasa*, 16°49′N, 24°52′W (PEICV and MNHN). **20** *Callhau*, 16°51′N, 24°52′W (PEICV, MNHN and FF). **21** *Baia das Gatas*, 16°54′N, 24°55′W (MNHN). **22** *Salamanza*, 16°54′N, 24°57′W (PEICV). **S. Luzia: 23** *Agua Doce*, 16°46′N, 24°48′W (PEICV). **24** *Curral*, 16°46′N, 24°48′W (ER). **25** *Off Praia Francisca*, 16°46′N, 24°47′W (−20 m dredging, PEICV). **26** *Between Ilhéu Branco and Ilhéu Raso*, 16°35′N, 24°40′W (−105 m, dredging no. 109 "Talisman", 1883, MNHN). **S. Nicolau: 27** *Tarrafal*, 16°30′N, 24°22′W (PEICV). **Boavista: 28** *Baia and Ilhéu de Sal Rei* (included Baia Teodora), 16°10′N, 22°56′W (PEICV, ER and FF). **29** *Morro da Areia* 16°03′N, 22°57′W (EM2 and FF). **30** *Baia da Gata*, 16°12′N, 22°40′W (ER). **31** 15°57′N, 22°44′W (−50 m dredging, RMNH). **Maio: 32** *Baia do Navio Quebrado*, 15°20′N, 23°10′W (ER). **33** *Ponta Pau Seco*, 15°15′N, 23°15′W (IIT and FF). **Santiago: 34** *Porto Praia and Ilha de S. Maria*, 14°55′N, 23°30′W (RMNH). **35** 14°54′N, 23°30′W (−75 to −68 m CANCAP–VI Sta. 6.005, −63 to −58 m CANCAP-VI. Sta. 6.004, −120 m CANCAP–VI Sta. 6.008, dredgings, RMNH). **36** *Prainha, Praia*, 14°55′N, 23°30′W (ER). **37** *Cidade Velha*, 14°55′N, 23°37′W (ER). **38** *Ponta Geneanes*, 14°57′N, 23°44′W (EM2) **39** *Baia de S. Clara*, 15°01′N, 23°44′W (−20 m scuba, RMNH). **40** *Baia Tarrafal*, 15°20′N, 23°44′W (EM2). **41** *Pedra Badejo*, 15°10′N, 23°35′W (EM2). **Fogo: 42** *Baia da Salina*, 15°02′N, 24°20′W (EM2). **43** 14°55′N, 24°31′W (−55 to −38 m CANCAP-VI. Sta. 6.040, dredging, RMNH). **Brava: 44** *Porto Anciāo*, 14°49′N, 24°46′W (EM2). **45** *Baia Pedrinha*, 14°55′N, 24°40′W (ER). **46** *Ilhéus Rombo o Secos (Ilhéu Grande)*, 14°58′N, 24°40′W (EM2). **S. Antão: 47** Locality unknown (MNHN).

Shell descriptions

The shell is smooth and glossy, and generally quite featureless. Most *Volvarina* species are quite similar in shape. Measurements were taken of the maximum shell length (L), from apex to anterior siphonal canal, maximum shell width (Ws) across the body whorl (Tab. 1), and the shell length/shell width ratio (L/Ws) was considered (Tab. 1 and Fig. 46). Shell size is often very valuable as a species–level character in Marginellids (Coovert & Coovert, 1995).

The paucispiral character of the protoconch in all the species studied here suggests a larval development intracapsular metamorphosis. Capacity for dispersion is therefore limited (Coovert, 1986: 14–15; Gofas & Fernandes, 1988: 3).

There are always four columellar plications. In all the species there was a weak longitudinal callus just posterior to the plications, more or less developed, but only in adult specimens.

The main interspecific differences were seen in the pigmented spiral bands of the body whorl. Their number, disposition, intensity and colour make up varied patterns which at first glance seem characteristic of different species. However, the species considered in this paper vary notably in pattern and number of bands on the shell in a manner reminiscent of the polymorphism of the extensively studied European landsnail *Cepaea* (Helicidae).

Some *Volvarina* species, mainly *V. taeniata* (Sal and S. Antão), *V. verdensis* (Boavista and Brava), and *V. nuriae* n. sp. (Boavista), can present two different tones of shell colour in a single population: straw-yellow and pink. In *Volvarina* species from Cape Verde Islands, the presence of two colours (straw and pink) in the same species was quoted for the first time by Jousseaume (1875: 56) (probably this observation of pink shells corresponds to *V. cessaci* Jousseaume, 1881= *V. taeniata*). The straw–yellow colour is the commonest among all the species, except *V. nuriae* n. sp. (more commonly the pink colour morph) and *V. boyeri* n. sp., (only with a purplish–pink colour). The pink colour is not present in populations of some species from some islands (e.g. *V. taeniata* from Brava, Santiago and Boavista), at least amongst the study material. Specimens or populations of *V. taeniata* (S. Vicente–S. Luzia) and *V. verdensis* (Fogo) have a shell with a brown colour, sometimes dark brown, that cannot be classified as "pink" or "straw". Finally, *V. mediocincta* and *V. corallina* shells are always brown or chestnut–coloured.

There may be up to six coloured bands numbered from 1 to 6 from suture to anterior end. The coloured bands are generally clustered in three groups. The posterior group, next to the suture, consists of only one, more or less broad, subsutural band (1). The middle cluster has 1 to 3 bands (2, 3 and 4), and the anterior cluster, next to the siphonal canal, has one or two (5 and 6) bands. The bands may be well defined, or more or less confluent with the adjacent ones. Bands 2 and 3, 2, 3 and 4, 5 and 6, or even 2 through 6 may be fused.

Colour bands in *Volvarina* will be described using a notation parallel to that used for *Cepaea* (Lang, 1904; Lamotte, 1951). P, S and B, respectively, will be used for "pink", "straw" and "brown" colours, 123456 for the six colour bands, and 0 for any missing band. A digit in lower case will indicate a weaker than normal band. "Sd" (abbreviation for spread) will denote a broader than normal band (M.A. Ramos, pers. comm.). Fused bands will be enclosed in brackets (square brackets if still recognizable). The position of the six bands is based on the *V. verdensis* specimens that show all them (Fig. 13, middle). This leads to a notation such as S-123456 or S–123056 for some specimens of *V. verdensis* on Boavista, P-1(23)4(56)Sd for specimens of *V. taeniata* on Sal, B-1(234)(56)Sd for most specimens of the same species on S. Vicente, etc. Sometimes bands may be missing, leaving a cluster with one band, as in *V. cernita, V. nuriae* n. sp. and *V. sauliae,* in which it is difficult to assign the correct position of bands 2, 3 and 4. In some *V. cernita* specimens, all the bands are missing, the shell being colourless (notation 000000). However,

the notation is useful to compare patterns between species or populations.

It is important to observe that in all the studied species (Cape Verde Island species and *V. obscura*) the bands are continuous over the outer lip (a very weak external varix), terminating with a more intense blotch thereon. In all the mainland species, the bands fade out before reaching the outer lip (outer lip lacking coloured blotches).

RADULA

The radulae were extracted from adult specimens using potassium hydroxide on whole animals soaked in water. Most radulae (55 specimens) were observed through a Nikon Optiphot microscope, then drawn with its camera lucida. One radula was mounted and observed with a scanning electron microscope (Fig 1).

All the species studied have a rachiglossan radula, reduced to a single central or rachidian tooth, quite broad, comb-like, and provided with a larger central cusp. The impressions of the cusps of the neighbouring tooth are visible (Fig. 1). There were 50–65 teeth per radula.

The following measurements were taken on the drawings (Fig. 2 and Tab. 2): tooth width (Wr), height of the central cusp (H), height of the lateral cusps (X) and height of the tooth base (Y). The cusps on each side of the central cusp were counted, and the shell length (L) was noted for specimens from which the radulae were extracted (Tab. 2). The following ratios were considered (Tab. 2): tooth width/height of central cusp (Wr/H), tooth width/number of cusps (Wr/cusps), and shell length/tooth width (L/Wr). The last ratio was used on several *Volvarina* species by Coovert & Coovert (1990).
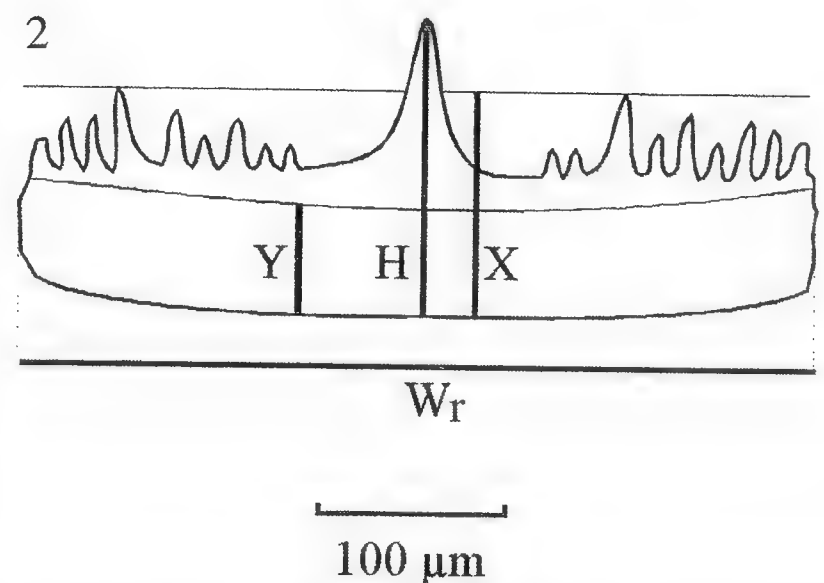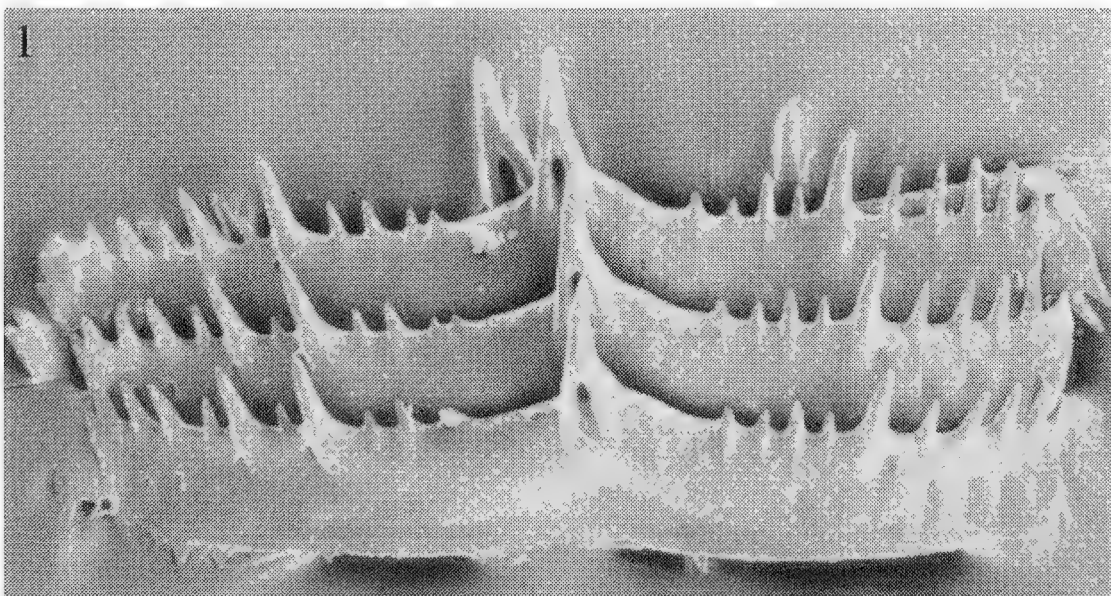
Figs 1–2 Radula of *Volvarina*. **1** Radula of *V. taeniata*, Ponta Preta, Sal (PEICV) (tooth width 357 µm). **2** Measurements taken: tooth width (Wr), height of central cusp (H), height of lateral cusps (X) and height of the tooth base (Y).

SYSTEMATIC DESCRIPTION

MARGINELLIDAE
MARGINELLINAE
PRUNINI

Genus   *Volvarina* Hinds, 1844
Type species   *Marginella nitida* Hinds, 1844

Definition   The shell of *Volvarina* is ovate-cylindrical, sometimes somewhat triangular as in *V. sauliae*, with a well–developed body whorl covering almost all the earlier whorls. It is always smooth and glossy due to the contact of the mantle which can be stretched out to cover the shell completely. The shell is translucent in the smaller species so that the inner mantle may be visible through the shell.

The protoconch is paucispiral as in all marginellids, and the adult shell has 3.0 to 4.5

whorls. The aperture is elongated and narrow and anteriorly has a broad, rounded siphonal canal. The columella always has four plications on its anterior half. The outer lip is always thickened in adults, and often, but not always, bordered externally by a very weak external varix.

The animal (Type 2) (Coovert, 1987) is very active, fast-moving, crawling on a large foot that is longer and broader than the shell when fully extended. The foot is truncated anteriorly and tapering posteriorly. The head is small, with a pair of tentacles set close together, quite long (1/4 of shell length), tapering, and carrying the eyes in small lateral bulges. The siphon lies over the head, is cleft on its lower side and is longer than the tentacles when fully extended. The mantle is smooth or rugose (tuberculate to papillose) (Coovert, 1987), and may cover the shell almost completely when the animal is undisturbed. Radula reduced to a single rachidian tooth (rachiglossa), quite broad, comb-like (Type 6) (Coovert, 1989). The pigmented areas are on the upper part of the foot, the head and tentacles, the siphon, and the mantle. The most common colours are black, brown, orange, pink, and opaque white. The tentacles, siphon and mantle edge are usually more brightly pigmented, while in many instances foot pigmentation is restricted to its anterior and posterior parts. When the animal is withdrawn, the pigmentation of the inner mantle may be seen through the shell.

Remarks   The radula is a useful character at the genus level in the family Marginellidae (Coan, 1965; Coovert, 1989; Coovert & Coovert, 1995), but is not very variable within a genus. In the case of Volvarina, there are some differences between species groups rather than between species, although "in some cases the radulae may serve to differentiate otherwise closely related or easily confused taxa" (Coovert & Coovert, 1990, p. 66). Radulae have been described with a prominent central cusp, as in *V. philippinarum* (Redfield, 1848), from Philippines (Coan, 1965; Coovert & Coovert, 1990), *V. obscura* of authors from Oman and SE Arabia (Coovert & Coovert, 1990), *V. insulana* Gofas & Fernandes, 1988, from S. Tomé and Principe islands (Fernandes & Rolán, 1991; Gofas & Fernandes, 1992), in the *V. rubella* complex, from the Caribbean (Coovert & Coovert, 1990), in *Volvarina* species from the Cape Verde islands (Coovert & Coovert, 1990, and herein), plus others in Coovert & Coovert (1990); or without a prominent central cusp, as in *V. taeniolata* Mörch, 1860, from Gulf of California (Fretter, 1976; Coovert & Coovert, 1990), *V. mitrella* (Risso, 1826), from Italy (Gofas, 1989), *V. ameliensis* (Tomlin, 1917), from Angola (Coovert & Coovert, 1990), and *V. riparia* Gofas & Fernandes, 1992, from Angola (Gofas & Fernandes, 1992), plus others in Coovert & Coovert (1990).

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Volvarina taeniata (Sowerby, 1846)
Figs. 1, 3–8, 40, 47, Map 2

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Marginella taeniata Sowerby, 1846a: 96 (unknown locality).
Volvarina cessaci Jousseaume, 1881: 187–188 (Cape Verde Is.).
Volvarina cessaci Rochebrune, 1881a: 30 (Porto Praia).
Volvarina quadripunctata Locard, 1897: 119, Pl. V, Figs. 7-9 (between Branco and Razo,
    Cape Verde Is., –105 m, dredging no. 109 "Talisman", 1883).
Volvarina taeniata Sowerby— Sowerby, 1846b: 391, pl. 76, Figs. 128–129.
Volvarina taeniata Sowerby— Jousseaume, 1875: 56; 1877: 270 (Cape Verde Is.).
Volvarina navicella (Reeve)— Jousseaume, 1875: 56; 1877: 270 (Cape Verde Is.).
Volvarina cessaci Rochebrune— Rochebrune, 1881b: 292–293, Fig. 14 (Porto Praia).
?Volvarina beyerleana (Bernardi, 1853)— Dautzenberg, 1900 (Branco).
Volvarina cessaci Jousseaume— Fischer–Piette & Beigbeder, 1944: 453 (Cape Verde Is.).
Marginella quadripunctata Locard— Fischer–Piette & Beigbeder, 1944: 457.
Marginella navicella Reeve— Marche-Marchad, 1956: 57 (Sal).

Volvarina rubella (C.B. Adams)— Kaicher, 1973: card 60 (Caribbean–Cape Verde Is.).
Marginella rubella C.B. Adams— Saunders, 1977: 14 (Sal and S. Vicente).
Marginella rubella navicella Reeve— Burnay and Monteiro, 1977: 43, Fig. 42 (Sal).
Marginella corallina Bavay— Burnay and Monteiro, 1977: 44, Fig. 44-45 (S. Vicente).
?*Volvarina beyerleana* (Bernardi, 1853)— Cosel, 1982b: 30 (Branco); Cosel, 1982c: 57 (Cape
    Verde Is. endemic ?).
Volvarina cf. *corallina* (Bavay)— Cosel, 1982 a: 20 (S. Vicente and Sal); 1982 c: 57 (Cape
    Verde Is. endemic).
Volvarina obscura (Reeve)— Cosel, 1982 a: 20 (Sal); 1982 c: 57 (Cape Verde Is. endemic).
Volvarina taeniata (Sowerby)— Cosel, 1982 a: 20 (Sal); 1982 c: 57 (Cape Verde Is. endemic).
Volvarina quadripunctata (Locard)— Cosel, 1982 b: 30 (between Branco and Razo).
Volvarina navicella Reeve— Cosel, 1982 c: 57 (Cape Verde Is. endemic).
Volvarina cessaci Rochebrune— Cosel, 1982 c: 57 (Cape Verde Is. endemic).
Volvarina corallina Bavay— Coovert, 1987: 18.
Volvarina cf. *taeniata* (Sowerby)— Coovert, 1987: 19.
Volvarina taeniata (Sowerby)— Kaicher, 1992: card 6149 (Cape Verde Is.).
Volvarina cessaci Jousseaume— Kaicher, 1992: card 6183 (Cape Verde Is.).
Volvarina taeniata (Sowerby)— Boyer, 1998: 8, Fig. 15 (photograph of animal).

Type material   *Marginella taeniata*: 3 syntypes, BMNH no. 1987046 (one specimen measuring 13.0 x 6.1 mm is here designated as lectotype, Fig. 3) (syntype figured by Kaicher, 1992: card 6149); *Volvarina cessaci* Jousseaume: 5 syntypes (Fig. 7), MNHN (one figured by Kaicher, 1992: card 6183); *Volvarina cessaci* Rochebrune: not found in MNHN; *Volvarina quadripunctata*: lectotype and two paralectotypes (the largest, broken), MNHN. The specimen 11.2 mm in length must be considered lectotype (Fig. 8) because Fischer–Piette & Beigbeder (1944: 457) cited it as "holotype", and the two specimens 11.8 and 12.1 mm, paralectotypes.

Other material examined   **Cape Verde Is.** 36 sh + 7 sh, no locality (MNHN, ER). **Boavista** 1 sh, Sal-Rei (UAM). **Brava** 5 sp, Baia Pedrinha (ER). **Sal** 2 sh + 1 sh + 2 sh + 10 sh, no locality (UAM, IIT, ER, MNHN). 6 sp, Joaquim Petinha (UAM). 4 sh, Ponta de Pedra Lume (ER). 14 sp, Rigona (UAM). 16 sp, Guincho do Ninho (UAM). 22 sp + 30 sh, Parda (UAM, MNHN). 3 sh, S. Maria (UAM). 27 sh, Ponta Preta (UAM). 3 sh + 55 sh, Palmeira (UAM, MNHN). 1 sh + 36 sh, Mordeira (UAM, MNHN). 1 sh, Palhona (UAM). 3 sp + 3 sp, Ponta de Leste (FF, ER). 18 sh, Algodoeiro (MNHN). 11 sh + 3 sh Fontona (MNHN, UAM). 10 sh, Baia Cerro Negro (MNHN). **S. Nicolau** 1 sh, Tarrafal (UAM). **S. Luzia** 2 sp, Agua Doce (UAM). **Santiago** 10 sh, no locality (MNHN). 1sh, 14°54'N, 23°30'W, CANCAP-VI, Sta. 6.005 (RMNH). 1 sh, 14°54'N, 23°30'W, CANCAP-VI, Sta. 6.008 (RMNH). **S. Antão** 43 sh, locality unknown (MNHN). **S. Vicente** 2 sh, 16°48'N, 25°06'W, CANCAP-VI, Sta. 6.146 (RMNH). 1 sp + 1 sh, Ilhéu dos Passaros (UAM, IIT). 1 sp + 2 sh + 1 sh, Matiota (UAM, ER, IIT). 3 sp, Ninho do Guincho (UAM). 2 sh, Baia das Gatas (UAM). 2 sh, Saragasa (MNHN). 2 sp, Salamanza (UAM). 1 sh, Callhau (MNHN).

Description   The shell dimensions are shown in Table 1 and Fig. 46. There are differences in shells between islands. The largest specimen measured was 15.3 mm maximum length (Sal). On Brava the shells were long and slender, and on S. Vicente and S. Luzia the specimens were smaller than on other islands. The shell has 3.5–4.5 whorls, and is ovate-cylindrical, with the broadest part slightly posterior to the midline. The thickening of the outer lip is defined by a very weak external varix and overrun by the termination of the pigmented bands. There are four columellar plications and a weak longitudinal callus (not always visible), just posterior to the plications. The shell is quite opaque, and the internal mantle hardly shows through.

V. taeniata has variable shell pigmentation. Two different tones are found in Sal and S. Antão specimens, pink and straw-yellow, the latter dominating by ⅔. On S. Vicente–S. Luzia, there are some dark brown specimens and pink shells are rare; on Brava, Santiago, S. Nicolau and Boavista, there are no pink specimens, at least amongst the study material. All six potential bands were never expressed separately at a time, but always some fusion of the bands occurred, at least between 2–3 and 5–6. Every island has its particular pattern frequencies:

• The typical pattern has some degree of fusion of central bands, with the notation 1(23)4(56)Sd (Fig. 4) and its variations 1Sd(23)4(56)Sd, 1(23)4(56)Sd and 1(23)0(56)Sd: Sal (231 sh), Santiago (8 sh), Brava (3 sh), S. Antão (30 sh), S. Nicolau (1 sh) and Boavista (1 sh).
• A characteristic pattern with complete fusion of all central bands, with the notation 1(234)(56)Sd (Fig. 5), sometimes very dark brown: S. Vicente (9 sh), S. Luzia (2 sh); and its variation 1[(23)4](56)Sd (Fig. 8): Branco and Razo (3 sh: lectotype and two paralectotypes of *V. quadripunctata*).
• A characteristic pattern with complete fusion of all central and anterior bands, with the notation 1(23456)Sd or 1[(23)(456)]Sd, which corresponds to the description of *V. cessaci*: Sal (8 sh), S. Vicente (1 sh, dark) (Burnay & Monteiro, 1977: Fig. 45, as *V. corallina*), and 5 syntypes of *V. cessaci* (Fig. 7) from Cape Verde Islands (from Porto Praia, Santiago, according to Rochebrune, 1881a and b).

A sinistral specimen is known (Palmeira, Sal, MNHN, leg. R. von Cosel), straw–coloured and with 13 mm shell length.

Live animal   The animal has rather diffuse pigmentation consisting of minute dots, with two coloured zones on the upper part of the foot, the anterior one being more intense than the posterior one (Fig. 40). It is brown-tinged with orange or pinkish tones on the anterior part. The whole upper part of the foot has scattered white dots. The siphon and tentacles are a more intense brown than the foot, particularly over the distal part. The siphon is covered in white spots and the tentacles have several white rings.

The edge of the outer mantle is dark brown, alternating with white patches. The surface of the outer mantle is slightly rugose and mottled with white and lighter brown. On S. Vicente island, the predominant colour is orange-brown, but the pattern is essentially the same.

Radula   The radular teeth (Figs. 1, 47, and Tab. 2) have a larger central cusp, with a broad smooth base, and the lateral cusps are well developed. The largest radula is 485 μm wide (Sal). The impressions of the cusps of the neighbouring tooth are visible (Fig. 1).The radulae of specimens from S. Vicente are smaller than those from Sal, but this correlates with a smaller shell size.

Geographic range and Habitat   The species was found on 8 out of 10 islands (Boavista, Brava, Sal, S. Luzia, S. Antão, Santiago, S. Nicolau and S. Vicente) and on two islets (Branco and Razo) (Map 2). It may also be found on the other islands, which were less thoroughly sampled. It is common on Sal, where it lives in the upper levels on the infralittoral and sometimes even in tidal pools. It is found in the sand lying under stones and coral slabs. On S. Vicente and S. Luzia, it is not so abundant and is mostly found at slightly deeper levels under 5 m, although it can also be found close to the shore. The most isolated populations seem to be those of the S. Vicente, S. Luzia, Branco, Razo island group, and those of Brava.

Comparisons and Remarks   *V. taeniata* is the largest species in the archipelago, which makes it easily recognizeable; only one of our specimens is smaller than the largest *V. verdensis*, the next largest species.

Figs 3–8 *Volvarina taeniata* (Sowerby, 1846): **3** *V. taeniata,* lectotype and paralectotype, locality unknown (BMNH) (13.0 x 6.1 mm and 13.0 x 5.6 mm), S–1(23)4(56)Sd. **4** *V. taeniata:* Joaquim Petinha, Sal (PEICV) (12.0 x 5.5 mm and 13.7 x 6.3 mm), S–1Sd(23)4(56)Sd. **5** *V. taeniata:* Matiota, S. Vicente (ER) (11.0 x 4.8 mm), B–1(234)(56)Sd. **6** *V. taeniata:* Baia Pedrinha, Brava (ER) (14.0 x 5.8 mm), S–1(23)4(56)Sd. **7** *V. cessaci* Jousseaume, 1881: syntypes, Cape Verde Is. (MNHN) (11.4 x 5.2 mm and 10.7 x 4.8 mm), S–1[(23)(456)]Sd. **8** *V. quadripunctata* Locard, 1897: lectotype, between Branco and Razo (MNHN) (11.2 x 4.8 mm), B–1[(23)4](56)Sd.

Shells from the islands of Sal, S. Nicolau, Boavista, Santiago and S. Antão are rather similar and resemble the types. The shells from Brava are more slender, and have the highest L/Ws ratio (2.41) of all the study populations. The pigmentation pattern with the union of bands 2 and 3, the union of bands 5 and 6, and with band 4 always present is different from all the other species except *V. boyeri* n. sp., but in the latter, band 4 is broader, and the colour is purplish–pink. A total fusion of all central and anterior bands 1(23456)Sd ("cessaci" pattern) was seen only in specimens of *V. taeniata* among all the species studied, except isolated specimens of *V. verdensis* from Fogo and of *V. corallina* from Santiago. The colour pattern of living animals and shell size are decisive to separate species.

On S. Vicente, S. Luzia, Branco and Razo, the shells are smaller and the colour pattern is different, with bands 2–4 fused. This pattern is similar to that of *V. verdensis* from Brava, but the animal's colour is different. A similar pattern (and colour) is seen in *V. corallina*, but *V. taeniata* is always much larger. Those *V. taeniata* shells from S. Vicente were considered as *V. corallina* by Burnay & Monteiro (1977), Cosel (1982a, c), and Coovert (1987) (see discussion of *V. corallina*).

The sinistral specimen of *V. taeniata* from the Cape Verde Islands quoted by Coovert & Lee (1989: 13, fide G. Saunders, pers. comm. to Lee) in L. Burnay's collection, is the same as that described in this paper (MNHN, leg. R. von Cosel). It was collected in Palmeira, Sal (31st December, 1978) during the expedition of R. von Cosel, E. Rolán and L. Burnay (December 1978–January 1979).

The animal was briefly described by Burnay & Monteiro (1977, as *M. rubella navicella* and *M. corallina),* see also Coovert (1987, as *Volvarina* cf. *taeniata* and *V. corallina),* and figured by Boyer (1998, photograph).

The radula is the largest among observed species, with a tooth width averaging 400 μm, but the shell length/tooth width ratio (L/Wr) may be larger in other species.

V. taeniata was described with an unknown locality (Sowerby, 1846a, b). Redfield (1869, 1870) believed, erroneously, that the species lived in the Bahamas and "West Indies", respectively. Jousseaume (1875, 1877) was the first to use the name *V. taeniata* for a species from Cape Verde archipelago. The syntypes are clearly conspecific with the largest Cape Verde Islands species and match our specimens from the islands of Santiago and Sal. It may be speculated that the syntypes were collected on Santiago, where the capital is located and which is the most easily visited locality on the archipelago. We have selected the 13.0 x 6.1 mm specimen as lectotype (BMNH no. 1987046) (Fig. 3, left); it has the pigmented spiral bands of the shell better preserved than the other syntypes, now paralectotypes.

The species name *V. cessaci* was introduced in the same year by two authors, Jousseaume (1881), and Rochebrune (1881a). The name of Jousseaume has priority, as it was published before (10th October, fide Tomlin, 1917). Rochebrune (1881a) cites his own work as "Séance du 29 octobre", and as an extract from his extensive paper on the Cape Verde Islands fauna (Rochebrune, 1881b). The former was published while the second was "sous presse" (in press), thus both references are later than the 10th October of Jousseume. Strangely, Jousseaume referred to this species (1877: 270) (material collected by M. de Cessac), but did not describe it. Both authors apparently used the same material for their descriptions, since both cited that M. de Cessac collected the material. Rochebrune (1881b: 293) said "Nous conservons à cette espèce le nom sous lequel M. le docteur Jousseaume se proposait de la publier (Bull. Soc. Zool. France 1877; p. 270)", referring to the Jousseaumme, 1877 material. Moreover, the types provided by Rochebrune are not in the MNHN collection. Fischer–Piette & Beigbeder (1944: 453) found the *V. cessaci* syntypes of Jousseaume in the MNHN, but not those of Rochebrune. Therefore, both names are apparently based on the same material and are herein considered objective synonyms. Curiously, Rochebrune (1881a and b) stated the type locality Porto

Praia (Santiago), while Jousseaume (1881) only cited Cape Verde Islands.

The name *V. rubella* (C.B. Adams, 1845), amply used in literature for this Cape Verde Islands species (Kaicher, 1973; Saunders, 1977; Burnay & Monteiro, 1977), corresponds to a Caribbean species (Coovert & Coovert, 1990: 58). The type locality is Jamaica, and the lectotype was designated and figured by Clench & Turner (1950: 248, Pl. 32, Fig. 4). The lectotype was also figured by Kaicher (1992: card 60/6195).

Some authors have associated the name *V. navicella* (Reeve, 1865) either with *V. rubella* (Redfield, 1869; Redfield, 1870; Tryon, 1882–83; Tomlin, 1917; Burnay & Monteiro, 1977) or with this Cape Verde Islands species (Jousseaume, 1875 and 1877; Marche–Marchad, 1956; Burnay & Monteiro, 1977; Cosel, 1982). The type locality of *V. navicella* is unknown, but on the label of the three syntypes (BMNH) "St. Thomas" was added later as quoted by Tomlin (1917). Reeve (1865) in the original description states: "Shell oblong–cylindrical, a little inflated, flesh–white, shining, obscurely four–banded with orange ...". In the Cape Verde species there are only four bands of colour in the largest species and in *V. boyeri* n. sp. Specimens of the largest species are conspecific with the syntypes of *V. taeniata* (see above) and differ from the syntypes of *V. navicella* (Fig. 9), especially in the shell proportions. The latter, which have no colour now, are smaller (10.7 x 5.3 mm; 8.6 x 4.3 mm and 8.1 x 4.1 mm) and shorter (mean of L/Ws= 1,99) than our specimens and the *V. taeniata* syntypes. The only Cape Verde species with the same shell length : width is *V. cernita*, which differs in only having three colour bands. This is possibly a species from the western Atlantic.

The name *V. beyerleana* (Bernardi, 1853), used for a Cape Verde Islands species by Dautzenberg (1910) and Cosel (1982b, c), corresponds to a Caribbean species (Jousseaume, 1875).

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Volvarina boyeri n. sp.
Figs. 10–11, Map 6

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Volvarina sp. 2— Boyer, 1998: 8, Fig. 17 (animal).

Holotype   1 sp collected by FB in August 1995, from Fontona, Sal, in MNHN. Animal figured by Boyer (1998: Fig. 17, as *Volvarina* sp. 2).

Paratypes   1 sp as holotype, in FB. 4 sh (paratypes 2–6) collected by R. von Cosel (MNHN, col. von Cosel, 31st December, 1978), from Palmeira (Pta. Joaquim Machado), Sal, in MNHN, MNCN and BMNH.

Type locality   Fontona, Sal, Cape Verde Islands, 4 m depth.

Other material examined   **Sal** 2 juv. as holotype (FB). 3 sh and 5 fg as paratypes 2–6 (MNHN). 2 sh, Palmeira (ER). 1 sh, Ponta Preta (PEICV). 1 sh, Ponta de Leste (FF).

Measurements (mm)

	Length (L)	Width (Ws)	L/Ws	Collection	Figure
Holotype	9.1	3.9	2.33	MNHN	10
Paratype 1	10.0	4.3	2.32	FB	——
Patatype 2	9.0	4.0	2.25	MNHN	11
Paratype 3	9.0	4.0	2.25	MNHN	——
Paratype 4	9.3	4.0	2.32	MNHN	——
Paratype 5	9.5	4.3	2.21	MNCN	——
Paratype 6	9.8	4.3	2.27	BMNH	——

Description   The dimensions are shown above, in Table 1 and Fig. 46. The shell has 3.5 whorls and is ovate–cylindrical. The outer lip is whitish and has a very weak external varix that shows the termination of the coloured bands. There are four columellar plications and a very weak longitudinal callus (not always visible), just posterior to the plications. The shell is somewhat translucent, and the animal is visible through it.

The pigmentation is always purplish–pink. There are four spiral bands on a pale, whitish unpigmented background; the anterior band is close to the siphonal notch, the posterior next to the suture, and the two median bands are broad and more or less equidistant. The bands are clearly marked over the thickened outer lip that presents four broad spots. The notation is 1Sd(23)4Sd(56) (Figs. 10 and 11) or its variation 1Sd[(23)4Sd](56).

Live animal The animal, figured by Boyer (1998), has the foot, tentacles and siphon uniformly pigmented with white, a very peculiar pattern lacking other colours.
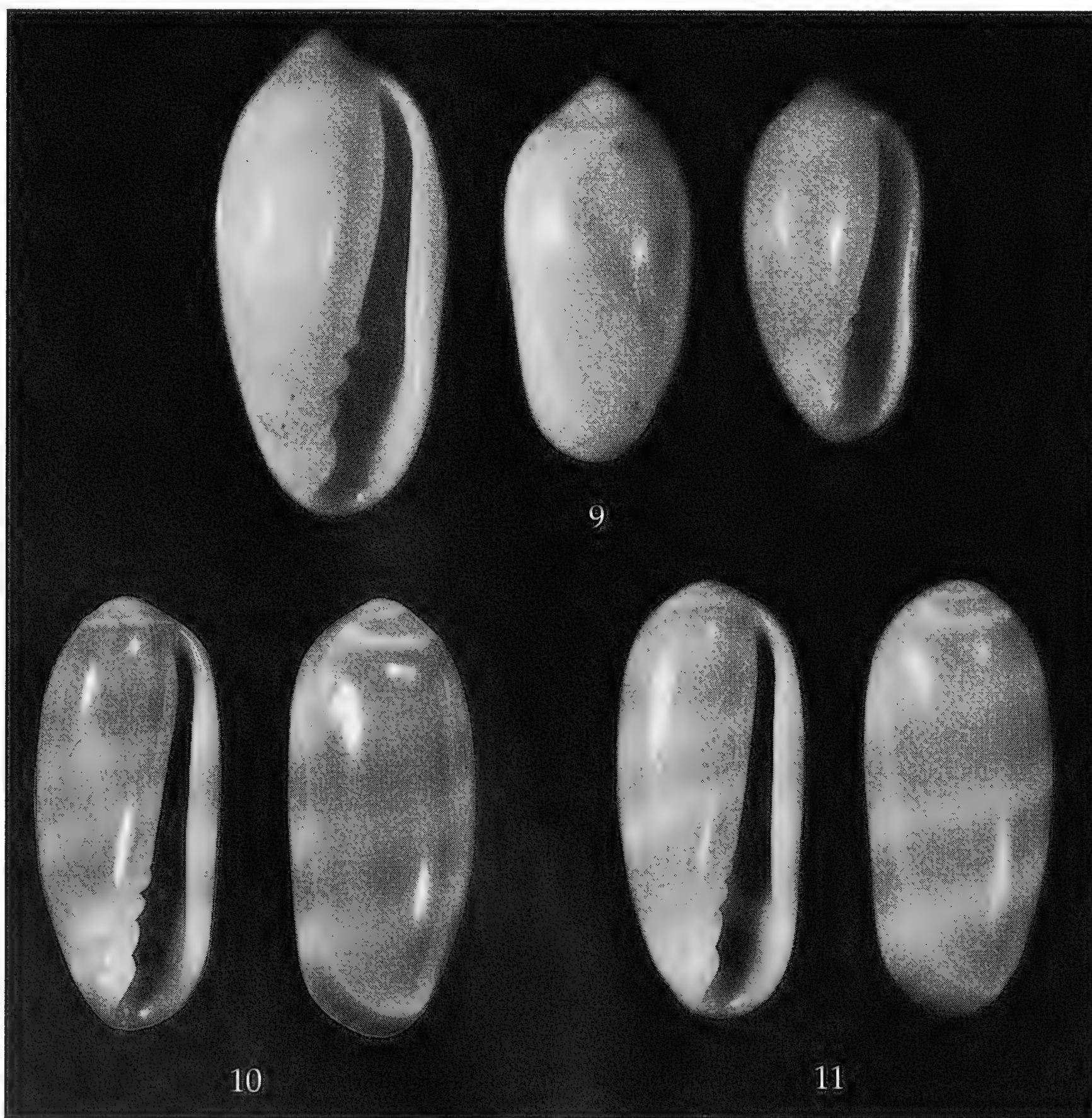

Fig. 9 *Volvarina navicella* (Reeve, 1865): three syntypes, locality unknown (BMNH) (10.7 x 5.3 mm, 8.6 x 4.3 mm, and 8.1 x 4.1 mm).
Figs 10–11 *Volvarina boyeri* n. sp.: **10** *V. boyeri* n. sp. holotype, Fontona, Sal (MNHN) (9.1 x 3.8 mm), P–1Sd(23)4Sd(56). **11** *V. boyeri* n. sp. paratype 2, Palmeira, Sal (MNHN) (9.0 x 4.0 mm), P– 1Sd(23)4Sd(56).

Radula   The radular teeth have not been studied.

Derivation of name   The species is dedicated to Franck **Boyer**, who figured the animal for the first time.

Geographic range and Habitat   This species was found only on the western coasts of Sal, mainly in the Fontona–Palmeira area (Map 6). The species lives as single (isolated) specimens under large stones covering fine gravels, from 4 m to deeper levels (F. Boyer pers. comm.).

Comparisons and Remarks   The shell pigmentation pattern with four broad bands and a colourless animal differentiates it from all other species from the Cape Verde Islands. *V. boyeri* n. sp. is always smaller than *V. taeniata*, and has four colour bands and is sympatric on the west coasts of Sal. Moreover, in *V. boyeri* n. sp. band 4 is broader than in *V. taeniata* and the colour is always purplish–pink, a rather different tone than *V. taeniata*.
   V. boyeri n. sp. is similar in size to *V. verdensis*, *V. nuriae* n. sp. and *V. joubini*, but differs in the colour pattern of the shell (has four broad colour bands), in the colour pattern of the animal (lacks dark dots), and in the distribution (*V. verdensis*, *V. nuriae* n. sp. and *V. joubini* are not present in Sal while *V. boyeri* n. sp. is a Sal endemic).
   V. boyeri n. sp. is usually larger than *V. cernita* (a sympatric species), and animal pigmentation is different (lacks black dots). It is always larger than *V. mediocincta*, *V. sauliae* (both sympatric with *V. boyeri* n. sp.) and *V. corallina*.
   The species lives in the same places and habitat as *V. taeniata* and *V. cernita*, but at deeper levels (from 4 m) (F. Boyer pers. comm.).
   The names *V. rubella* (C.B. Adams, 1845) and *V. navicella* (Reeve, 1865), amply used in the literature for CapeVerde Island species, were discussed above (see Comparisons and Remarks of *V. taeniata*). *V. rubella* is a Caribbean species (Coovert & Coovert, 1990). *V. navicella* (Reeve, 1865) was described with four bands on the body whorl and similar in size to *V. boyeri* n. sp., but in the former the shell is broader, tapers anteriorly, and the colour is different (orange).

<h2 style="text-align:center">***Volvarina verdensis*** (E.A. Smith, 1875)
Figs. 12–18, 41, 48, Map 3</h2>

Marginella (Volvarina) verdensis E.A. Smith, 1875: p. 200 (Cape Verde Is.).
Volvarina taeniata var. *minor* Jousseaume, 1877: 270 (Cape Verde Is.).
Marginella (Volvarina) verdensis E.A. Smith— Tomlin, 1917: 304 (C. Verdes).
Volvarina taeniata var. *minor* Jousseaume— Tomlin, 1917: 270 (= V. verdensis).
Marginella taeniata var. *verdensis* E.A. Smith— Marche-Marchad, 1956: 57 (Santiago).
Volvarina verdensis (E.A. Smith)— Coovert & Coovert, 1990: 63, Fig. 146 (radula).
Volvarina verdensis (E.A. Smith)— Kaicher, 1992: card 6121 (Cape Verde Is.).

Type material   *Marginella verdensis:* 3 syntypes (the specimen measuring 9.8 x 4.6 mm is designated here as lectotype, Fig. 12, right), BMNH no. 18744255 (syntype figured by Kaicher, 1992: card 6121). *Volvarina taeniata* var. *minor:* not found in MNHN.

Other material examined   **Cape Verde Is.** 49 sh, no locality (MNHN). **Boavista** 5 sh + 3 sh, no locality (ER, FF). 73 sp + 7 sp + 25 sh + 14 sp, Sal-Rei (UAM, ER, IIT, FF). 3 juv. + 4 sp, Morro da Areia (EM2, FF). **Brava** 11 sp, Baia Pedrinha (ER). 3 sp, Porto Ancião (EM2). 5 sp, Ilhéus Rombo o Secos, Ilhéu Grande (EM2). **Fogo** 8 sp, Baia da Salina (EM2). **Maio** 2 sh, no locality (ER). 1 sh, Pau-Seco (IIT). **Santiago** 5 sh + 40 sh, Praia (ER,

MNHN). 2 sh, 14°55'N, 23°30'W, CANCAP-VI, Sta. 6.406 (RMNH). 1 sh, 14°54'N, 23°30'W, CANCAP-VI Sta. 6.003 (RMNH). 4 sh, Cidade Velha (ER). 6 sp, Pedra Badejo (EM2). 23 sp, Ponta Geneanes (EM2). 13 sp, Baia Tarrafal (EM2).

Description   The shell dimensions are shown in Table 1 and Fig. 46. There are few diffe-rences in shell size among islands. On Santiago, shells are smaller (mean) than in spec-imens from Boavista, Brava and Maio. The shell has 3.5-4 whorls and is cylindrical with a rather straight outer lip. The thickening of the outer lip is slight, with a very weak external varix, and shows the termination of the coloured bands. There are four columel-lar plications and a very weak longitudinal callus (not always visible) just posterior to the plications. The shell is somewhat translucent, the animal being visible through it.

Shell pigmentation may be straw-yellow or pink, the former being more frequent, about ⅔ on Boavista and ¾ on Brava. On Santiago and Maio, there are no pink speci-mens, at least among the study material, and on Fogo they are brown. There may be up to six spiral bands expressed in this species. Every island has its particular pattern frequencies:

- The simple pattern with all six bands differentiated and the notation 123456 was found only on Boavista (32 sh). Variations of this pattern such as 1Sd23456Sd (Fig. 13, middle), 1Sd23456Sd (Fig. 13, right), 123056Sd, 123456Sd, 1Sd23456, 123056, 123456, 123456, 123056, 123450, and 123456, were found at least once on Boavista (22 sh) or Santiago (7 sh).
- Patterns with fused bands in the central area are 1[23]456Sd, 1Sd[23]456, and 1Sd[234]56, were found only on Boavista (3 sh).
- Patterns with fused anterior bands and notations as 1234(56), 1234(56)Sd, 1234[56]Sd, 1Sd234[56]Sd, and 1Sd204[56] were found on Boavista (6 sh), Santiago (22 sh), and in the lectotype (Fig. 12 right).
- Patterns with some degree of fusion of both central and anterior bands are 1Sd[23]4[56Sd] and 1Sd(23)4(56)Sd: Boavista (1 sh) and Santiago (17 sh).
- A characteristic pattern with some degree of fusion of both central and anterior bands, and the notation 1Sd2(34)[56Sd] was found only on Maio (3 sh) (Fig. 14) and the eastern coast of Santiago (Pedra Badejo) (4 sh) (Fig. 15).
- Patterns with a more complete fusion of all central and anterior bands, with the nota-tions 1(234)(56)Sd, 1Sd(234)(56)Sd, and 1[(23)4](56)Sd, and its variations 1Sd[234](56)Sd and 1[234](56)Sd, were found principally on Brava (18 sh) (Figs. 16 and 17), but also in Santiago (3 sh) and Boavista (3 sh, only variations).
- A complete fusion of all bands with the notations (123456)Sd (Fig. 18), [1(23456Sd)], and [1(234)(56)Sd], was found only on Fogo (3 sh, 1 sh and 1 sh, respectively).

Live animal   The animal (Fig. 41) was observed on Boavista (PEICV) and on Santiago, Fogo and Brava (E. Rolán pers. comm). The upper part of its foot is covered in small brown dots and tiny black dots. Pigmentation is more intense on the anterior and poste-rior parts of the foot. The tentacles and siphon have larger brown spots. The surface of the outer mantle was not observed. The edge of the outer mantle has dark brown patches alternating with white; the inner mantle seen through the transparent shell has large dark patches.

Radula   The teeth are broad and the central cusp does not protrude very much (Fig. 48 and Tab. 2). There are more than 12 lateral cusps on each side (average) that reach the base of the central cusp. See also Coovert & Coovert (1990: 63–64).

Geographic range and Habitat   The species is common on Boavista and Santiago, and not as common on Brava, Fogo and Maio (Map 3). It lives in shallow water in the upper
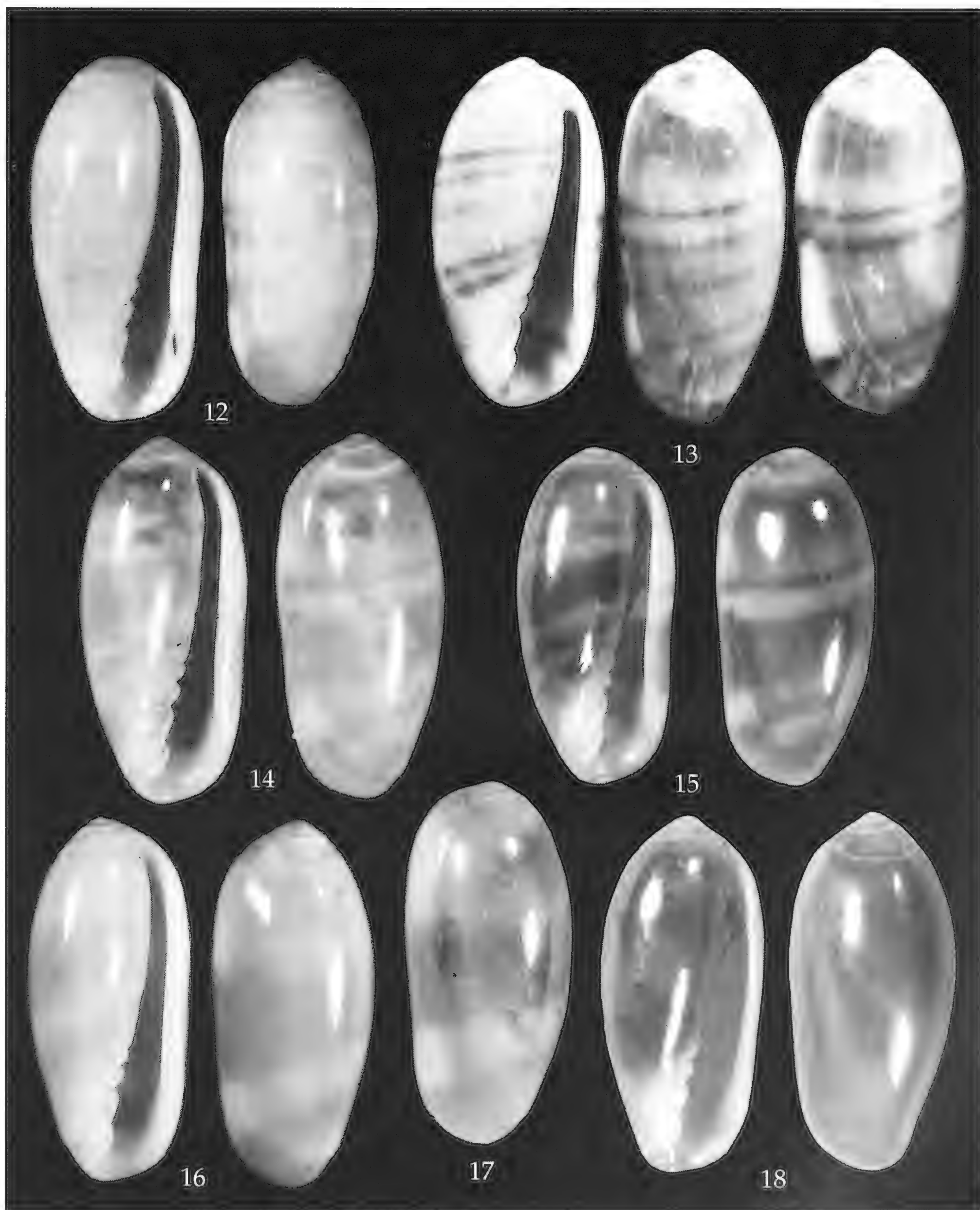
Figs 12–18 *Volvarina verdensis* (E.A. Smith, 1875): **12** *V. verdensis,* paralectotype and lectotype, Cape Verde Is. (BMNH) (10.4 x 4.9 mm and 9.8 x 4.6 mm), S–1234(56)Sd. **13** *V. verdensis:* Sal Rei, Boavista (PEICV) (9.1 x 4.2 mm, 9.5 x 4.6 mm and 9.3 x 4.4 mm), S–1Sd23456Sd and S–1Sd23456Sd. **14** *V. verdensis:* Baia do Navio Quebrado, Maio (ER) (9.9 x 4.6 mm), S–1Sd2(34)[56Sd]. **15** *V. verdensis:* Pedra Badejo, Santiago (EM2) (9.5 x 4.4 mm), S–1Sd2(34)[56Sd]. **16** *V. verdensis:* Baia Pedrinha, Brava (ER) (10.3 x 4.6 mm), R–1(234)(56). **17** *V. verdensis:* Porto Ancião, Brava (EM2) (10.1 x 4.7 mm), S–1(234)(56)Sd. **18** *V. verdensis:* Baia Salinas, Fogo (EM2) (9.0 x 4.2 mm), B–(123456)Sd.

levels of the infralittoral to a depth of 3–4 m on rocky bottoms in sand under stones. On Fogo, shells are almost uniformly dark, probably due to the black colour of the volcanic rocks (E. Rolán, pers. comm.).

Comparisons and Remarks   This is the second largest species in the archipelago after *V. taeniata;* only one of our specimens is larger than the smallest *V. taeniata*. The specimens from Santiago are somewhat smaller than average size. The shell of *V. verdensis* is more cylindrical than the other species studied, except *V. boyeri* n. sp. and *V. corallina,* and its outline is not so oval due to the straight outer lip.

V. verdensis is similar in size to *V. boyeri* n. sp,. *V. nuriae* and *V. joubini,* but differs in the colour pattern of the shell (usually six bands; if it has three bands they are very broad), and in the colour pattern of the animal (with black and brown dots). Moreover, *V. verdenisis* has an allopatric distribution with *V. boyeri* n. sp. (a Sal endemic).

It is usually larger than *V. cernita* and *V. sauliae,* both sympatric species. Animal pattern is similar to that of *V. cernita,* but differs in having more brown dots than black ones unlike the latter species. Moreover, the shell pattern of *V. cernita* has only three bands (usually 103050).

V. verdensis is always larger than *V. mediocincta* and *V. corallina*. These species have a very different animal pigmentation pattern, lacking dark dots.

The basic pattern with six bands was only seen on *V. verdensis*. Patterns with a simple fusion of both central and anterior bands 1(23)4(56)Sd were not usually seen in this species, and are characteristic of *V. taeniata* on some islands. A pattern with a complete fusion of all central bands, as 1(234)(56)Sd, is typical of specimens from Brava, but also of *V. taeniata* shells from S. Vicente and S. Luzia, and similar to those of *V. corallina*. A pattern with a total fusion of all central and anterior bands similar to the "cessaci" pattern of *V. taeniata* was only seen on specimens from Fogo. Other *V. verdensis* specimens from Fogo show a total fusion of bands (123456)Sd never seen in other species. The colour pattern of living animals and shell size are decisive for separating the species.

The radular teeth were studied and figured by Coovert & Coovert (1990: 63, Fig.146), and our data are almost identical. The shell length/tooth width ratio (L/Wr= 25.39) is the smallest among all the species studied (except populations of *V. cernita* from S. Vicente and S. Luzia), showing a relatively large radula. *V. verdensis* has a comparatively small central cusp with a lower Wr/H ratio (average is 3.23) and the highest number of lateral cusps among all the study species (more than 12). Lateral cusps reaching the base of the central cusp were never seen in other study species, except *V. sauliae,* with smaller radular teeth.

We have selected the 9.8 x 4.6 mm *V. verdensis* specimen as lectotype (BMNH no. 18744255) (Fig. 12, right). It has the pigmented spiral bands of the shell better preserved than the other syntypes, which now become paralectotypes.

The type specimens could have originated from Santiago, where the species is abundant, since the predominant banding pattern is very similar to that of the lectotype, with the notation 1234(56)Sd (a fusion of anterior bands). As the capital is located there, Santiago may have been the most likely place of origin, but all the specimens observed there are smaller than the types (Tab. 1); its size is more similar to that of the specimens from Boavista. Further support for the origin of the types from Boavista, an island of the northern group, is the simultaneous description of *V. verdensis* and *V. mediocincta* by E.A. Smith from specimens collected by P. Furse. *V. mediocincta* had hitherto not been found on Santiago, but mainly on islands of the northern group Sal, Boavista and S. Vicente. On other islands (Maio and Brava), the pattern is so different that there is no possible confusion.

Jousseaume (1877) named *V. taeniata* var. *minor* in a list of the known Marginellids of the Cape Verde Islands. Tomlin (1917) believed that this name is a synonym of *V. verden-*

sis, and we agree. Jousseaume (1877) mentioned a large number of specimens collected by M. de Cessac in Cape Verde Islands. These shells may have originated from Santiago or Boavista, where the species is abundant, but the dimensions given (8.0 x 3.5 mm) best fit our own observations on Santiago (Tab. 1). Moreover, other specimens collected by M. de Cessac come from Santiago, e.g. the type material of *V. cessaci* Rochebrune, 1881 (Porto Praia) (see Comparisons and Remarks of *V. taeniata).*

Volvarina mediocincta (E.A. Smith, 1875)
Figs. 19–22, 42, 49, Map 4

Marginella (Volvarina) mediocincta E.A. Smith, 1875: 201 (Cape Verde Is.).
Volvarina bouvieri Jousseaume, 1877: 268, pl. 5, Figs. 5–7 (Cape Verde Is.).
Marginella (Volvarina) corallina Bavay, 1910— Roth and Clover, 1973: 210 (considered possible synonym of *V. mediocincta).*
Marginella (Volvarina) mediocincta E.A. Smith— Tomlin, 1917: 279 (Cape Verdes).
Volvarina mediocincta (E.A. Smith)— Cosel, 1982a: 20 (S.Vicente, Sal, Boavista); 1982c: 57 (Cape Verde Is. endemic)..
Volvarina mediocincta (E.A. Smith)— Kaicher, 1992: card 6119 (Cape Verde Is.).
Volvarina bouvieri Jousseaume— Kaicher, 1992: card 6165 (? Cape Verde Is.).
Volvarina mediocincta (E.A. Smith)— Boyer, 1998: 11, Fig. 14 (animal).
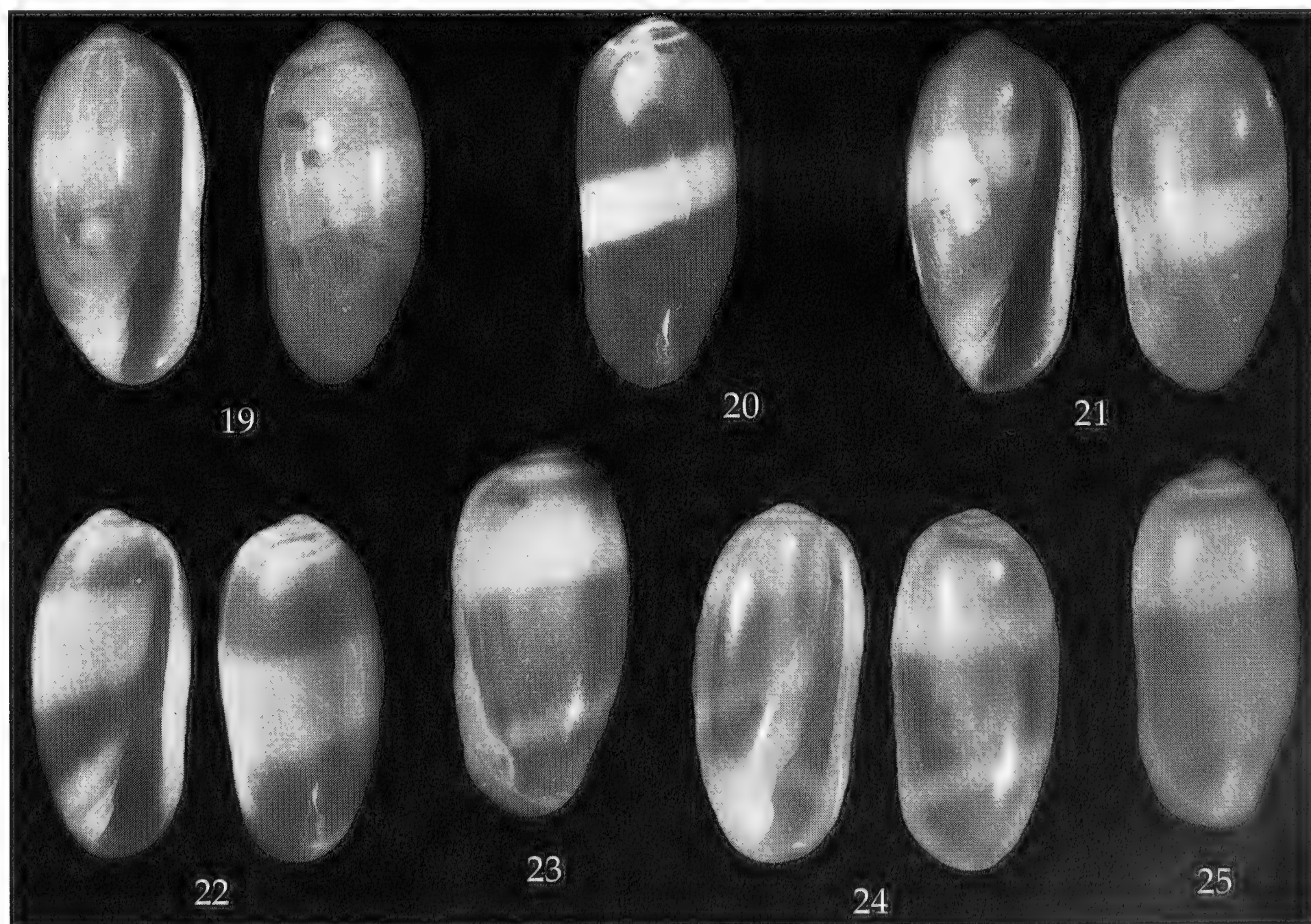
Figs 19–22 *Volvarina mediocincta* (E.A. Smith, 1875): **19** *V. mediocincta,* paralectotype and lectotype, Cape Verde Is. (BMNH) (6.5 x 3.1 mm and 6.4 x 3.0 mm), B–(123)(456)Sd.. **20** *V. mediocincta:* Palmeira, Sal (PEICV) (5.9 x 2.6 mm and 6.0 x 2.7 mm), B–(123)(456)Sd. **21** *V. bouvieri* (Jousseaume, 1877): syntype, Cape Verde Is. (MNHN) (5.5 x 2.7 mm), B–(123)(456)Sd. **22** *V. mediocincta:* Rigona, Sal (PEICV) (6.1 x 2.7 mm), B–(12)00(56)Sd.
Figs 23–25 *Volvarina corallina* (Bavay, 1910): **23** *V. corallina:* syntype, Cape Verde Is. (MNHN) (5.0 x 2.4 mm), B–1(234)Sd(56)Sd (Photograph of MNHN). **24** *V. corallina:* Tarrafal, Santiago (MNHN) (6.6 x 3.1mm), B–1(234)Sd(56)Sd. **25** *V. corallina:* Baia Pedrinha, Brava (ER) (5.7 x 2.7 mm), B– 1[(234)Sd(56)Sd].

Type material   Marginella mediocincta: 2 syntypes (Fig. 19) (the specimen measuring 6.4 x 3.0 mm is designated here as lectotype) BMNH no. 18744256 (syntype figured by Kaicher, 1992: card 6119). *Volvarina bouvieri:* one probable syntype (Fig. 21) MNHN (figured by Kaicher, 1992: card 6165).

Other material examined   **Cape Verde Is.** 2 sh, no locality (MNHN). **Boavista** 1 sh, Sal Rei (FF). 1 sh, Baia da Gata (ER). **Brava** 1 fg, Baia Pedrinha (ER). **Sal** 2 sh, Baia Cerro Negro (MNHN). 6 sh, Mordeira (MNHN). 2 sp + 17 sh , Palmeira (UAM, MNHN). 2 sh + 3 sh, Parda (ER, MNHN). 2 sp, Rigona (UAM). **S. Vicente** 1 sh + 1 sh Callhau (UAM, MNHN). 3 sp, Salamanza (UAM).

Description   The shell dimensions are shown in Table 1 and Fig. 46. The shell is small, has 3.0–3.5 whorls, and is ovate-cylindrical. The thickening of the outer lip is poorly developed, with a very weak external varix, and shows the termination of the coloured bands. There are four columellar plications and a very slight longitudinal callus (not always visible) just posterior to the plications. The shell is somewhat translucent and the animal is visible through it.

Shell colour is distinctive with generally very dark brown pigmentation limited to the anterior and posterior parts, and a median, well defined colourless area which is alluded to by the specific epithet. The only observed variation involves the intensity of the brown pigmentation; on some specimens it was a paler brown with a broader and more poorly defined median area.

The notation of the particular pattern of this species is: B–(123)(456)Sd (Fig. 20) or B–(12)00(56)Sd (Fig. 22).

Live animal   It has distinctive pigmentation (Fig. 42), pale with orange spots distributed on the posterior part of the foot (1 spot), on the anterior part (1 or 2 spots on each side), on the tentacles (1 or 2 on each), and on the siphon (1 or 2). Specimens with paler shell pigmentation also have fewer spots. The surface of the outer mantle was not observed; its edge is unpigmented.

Radula   The radular teeth have a larger central cusp, with a broad smooth base (Fig. 49 and Tab. 2). There are few small lateral cusps (average 8.3\8.2).

Geographic range and Habitat The species was collected mainly on the northern islands: Sal, S. Vicente, and Boavista, uncommon on the latter island (Map 4). On Sal and S. Vicente, it is never as abundant as the other species, as noted already by Jousseaume (1877: 269) from the data of Bouvier and M. de Cessac, when describing *V. bouvieri*. On the southern islands it was only collected on Brava (1 broken specimen). It lives in shallow water, in the upper part of the infralittoral, in areas of rocks with sand.

Comparisons and Remarks This unmistakable species has a colour pattern that is the inverse of the usual one, with brown pigmentation limited to the anterior and posterior parts. It is the smallest species in the archipelago, except for a few specimens of *V. corallina* and *V. cernita*. The outer lip is less thickened than in the other species.

The animal pattern is also peculiar and different from all the other studied species. The radular teeth are similar in form, proportions, and L/Wr ratio to those of *V. taeniata*, but smaller and with the lateral cusps not very developed.

There are no particular problems with the syntypes of *V. mediocincta* and *V. bouvieri*. Due to the species' very homogeneous morphology it is not possible to infer their place of origin more accurately.

We have selected the 6.4 x 3.0 mm *V. mediocincta* specimen as lectotype (BMNH no.

18744256) (Fig. 19, right). This specimen has the pigmented spiral bands of the shell better preserved than the other syntype, now considered a paralectotype.

Roth & Clover (1973) considered *V. corallina* Bavay, 1910 a probable synonym of *V. mediocincta* based on the general appearance of the shell and the similar size. We disagree because the banding patterns are so different that we cannot encompass them in the usual intraspecific variation. *V. corallina* has three dark bands, one of which is median, alternating with two pale bands, whereas *V. mediocincta* has a pale central band. The animal colour pattern is different in both species, with differentiated orange spots in *V. mediocincta* (foot, tentacles and siphon), while in *V. corallina* there are areas with small orange dots.

Volvarina corallina (Bavay, 1910)
Figs. 23–25, 43, Map 6

Marginella (Volvarina) corallina Bavay, 1910: 22, pl. I, Figs. 1–2.
Volvarina corallina (Bavay)— Kaicher, 1992: card 6182 (Cape Verde Is.).

Type material   Marginella (Volvarina) corallina: 1 syntype MNHN (Fig. 23) (figured by Kaicher, 1992: card 6182).

*Other material examined   **Brava** 1 sp, Baia Pedrinha (ER). **Santiago** 2 sp, Ponta Geneanes (EM2). 7 sp and 2 juv., Baia Tarrafal (EM2).

*Description   The shell dimensions are shown in Table 1 and Fig. 46. The shell is small, has 3–3.5 whorls, and is ovate–cylindrical. The thickening of the outer lip is poorly developed, with a very weak external varix, and shows the termination of the coloured bands. There are four columellar plications and a very weak longitudinal callus (not always visible), just posterior to the plications. The shell is somewhat translucent, and the animal is visible through it.

The shell colour is peculiar, always with reddish–brown pigmentation (red in the original description by Bavay (1910)) on a pale, whitish unpigmented background. There are three spirals bands, the anterior close to the siphonal notch, the medial very broad and the posterior next to the suture. The pigmentation pattern has a few variations:
  • A characteristic pattern with fusion in both central and anterior areas, with the notation 1(234)Sd(56)Sd, was found in the syntype (unknown locality) (Fig. 23), and on Santiago (9 sh) (Fig. 24).
  • A pattern with a complete fusion of all central and anterior bands, with the notation 1(23456)Sd, was found on Santiago (2 sh). The variation: 1[(234)Sd(56)Sd] (Fig. 25) was seen on Brava (1 sh).

*Live animal   The animal (from sketches of E. Rolán) is pale with many orange dots in the propodium and in the posterior part of the foot, and a few dots on the lateral parts (Fig. 43). Some specimens have a brownish colour in the propodium, together with orange dots. There are also white spots on the posterior part of the foot. The tentacles have orange dots and on the siphon orange dots and white spots. The outer mantle is pale or has scattered orange dots, but the morphology of the surface was not observed. The edge of the mantle is brown alternating with white patches. Sometimes the internal mantle is seen through the shell and has irregular dark areas on a pale background. Specimens from Santiago and Brava have the same pattern (E. Rolán, pers. comm.).

*Radula   Radular teeth have not been studied.

Geographic range and Habitat   The species has been found only on the western coast of Santiago and on Brava (Map 6). *V. corallina* lives in sand under large stones at a depth of 3–4 m (E. Rolán, pers. comm.).

Comparisons and Remarks   The size (mean) of *V. corallina* is smaller than all the other species from the Cape Verde Islands except *V. mediocincta,* but the colour pattern (shell and animal) are different. *V. corallina* was considered by Roth & Clover (1973) as a synonym of *V. mediocincta,* a view with which we disagree (see notes under that species). The size and the reddish–brown colour of the shell are similar to that of *V. mediocincta,* but the band pattern of the shell and the colour pattern of the animal are different and consistent in both species. There are a few samples of *V. corallina,* only from the southern islands (Santiago and Brava), but both species are sympatric, at least on Brava.

With regard to *V. cernita,* there are only a few shells with a similar length, and some specimens have a band pattern also similar to that of *V. corallina,* with a broad middle band (Figs. 30 and 31). In these circumstances the animal's colour pattern was decisive to separate both species.

The colour pattern of the shell is similar to that of specimens of *V. taeniata* from S. Vicente–S. Luzia, with three broad bands, but the specimens of *V. taeniata* are always much larger. *V. taeniata* shells from S. Vicente, that were considered as *V. corallina* by Burnay & Monteiro (1977), Cosel (1982a, c), and Coovert (1987), show notations such as 1(234)(56)Sd to 1(23456)Sd, with two tones, dark brown and pink (see description of *V. taeniata),* while *V. corallina* specimens have patterns such as 1Sd(234)Sd(56)Sd or 1Sd(23456)Sd (note the Sd after bands 1 and 4) and are always brown. The pigmentation pattern and colour of the *V. corallina* animal and specimens of *V. taeniata* from S. Vicente–S. Luzia are also similar. The latter could be considered a giant form of *V. corallina* or a variation of *V. taeniata.* We prefer to consider them as a form of *V. taeniata,* a species present on all the other neighbouring islands, but not on S. Vicente–S. Luzia. The size is more or less within the range of variation of other *V. taeniata* populations, and there are intermediate forms between Sal and S. Vicente–S. Luzia patterns, such as the *V. quadripunctata* types with the notation 1[(23)4](56)Sd.

The syntype of *V. corallina* is a very small shell (5.0 mm length) while the smallest adult in our material is 5.7 mm long, but the peculiar band pattern of our specimens is identical to that of the syntype.

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Volvarina cernita (Locard, 1897)
Figs. 26–31, 44, 50–51, Map 5

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Marginella cernita Locard, 1897: p. 120; Pl. IV, Figs. 10 - 12 (S. Vicente).
Volvarina tribalteata Reeve, 1865— Jousseaume, 1875: 55; 1877: 270 (Cape Verde Is.).
?Volvarina sauliae (Sowerby, 1846)— Rochebrune, 1881b: 293 (Porto Praia and S. Vicente).
Marginella cernita Locard— Tomlin, 1917: 258 (–20 m, S. Vicente, C. Verde Is.).
Marginella cernita Locard— Fischer–Piette & Beigbeder, 1944: 453 (Cape Verde Is.).
Marginella exilis (Gmelin)— Knudsen, 1956 (Cape Verde Is.).
Marginella mitrella Risso— Saunders, 1977: 14 (S. Vicente).
Marginella sp.— Burnay and Monteiro, 1977: 45, Fig. 46 (Sal).
Volvarina exilis (Gmelin)— Cosel, 1982c: 57 (Cape Verde Is.).
Volvarina mitrella (Risso)— Cosel, 1982c: 57 (Cape Verde Is.).
Volvarina sp.— Coovert, 1987: 19.
Volvarina sp. 1— Boyer, 1998: 8, Fig. 16 (photograph of animal).

Type material   *Marginella cernita:* 1 syntype MNHN (Fig. 26).

Other material examined **Cape Verde Is.** 14 sh, no locality (MNHN). **Boavista** 2 sh, No locality (ER). 36 sp + 2 sh + 4 sp, Sal-Rei (UAM, IIT, EM2). 2 sh, 15°57'N, 22°44'W, CANCAP-VI, Sta. 6.059 (RMNH). 5 sp, Morro Areia (FF). **Brava** 2 sp, Porto Ancião (EM2). **Fogo** 1 sh, 14°55'N, 24°31'W, CANCAP-VI, Sta. 6.040 (RMNH). **Maio** 1 sh, Pau Seco (FF). **Sal** 3 sh + 50 sh, no locality (ER, MNHN). 2 sp + 10 sh + 6 sh, Palmeira (UAM, MNHN, FF). 1 sp + 4 sh , Parda (UAM, MNHN). 14 sp, Rigona (UAM). 21 sh, Algodoeiro (MNHN). 16 sh, Mordeira (MNHN). 15 sh, Baia Cerro Negro (MNHN). 1 sh, Fontona (MNHN). 3 sp, Guincho do Ninho (UAM). **S. Nicolau** 2 sh, Tarrafal (UAM). **S. Luzia** 1 sp, off Praia Francisca (UAM). 3 sp, Agua Doce (UAM). 2 sh, Curral (ER). **Santiago** 2 sh, Baia S. Clara (RMNH). 1 sh, 14°54'N, 23°30'W, CANCAP-VI. Sta. 6.004 (RMNH). 1sp, Baia Tarrafal (EM2). **S. Antão** 2 sp, no locality (MNHN). **S. Vicente** 3 sp, Ninho do Guincho (UAM). 6 sp + 10 sh + 1 sh, Callhau (UAM, MNHN, FF). 15 sp + 1 sh , Salamanza (UAM, MNHN). 5 sp + 11 sh , Saragasa (UAM, MNHN). 1 sp, Ilhéu dos Passaros (UAM). 1 sh + 2 sh, Porto Mindelo (UAM, FF).

Description   This species is quite variable in size and proportions (Table 1 and Fig. 46). On Sal, Boavista, S. Vicente and S. Antão the measurements average 7.0 mm, while on S. Luzia the shells are very large, averaging 8.4 mm (although in this locality there are also smaller shells, 5.8 mm length). The smallest specimen is 5.1 mm long (syntype). The shell is always broad, with a L/Ws ratio under 2 (means). The shell has 3.5–4 whorls, is ovate-cylindrical, and the protoconch is pale. The thickening of the outer lip is slight, with a weak external varix, and shows the termination of the coloured bands. There are four columellar plications and a very weak longitudinal callus (not always visible), just posterior to the plications. The shell is somewhat translucent, and the inner mantle is visible.

The shell pigmentation is variable. There is a typical pattern with three straw–coloured bands, rarely pink, more or less narrow, but always narrower than the colourless areas between them. On all the islands, and usually in S. Vicente and S. Luzia specimens, the bands are generally well-defined lines, and the typical notation is 103050, and its variations 103Sd050, 103Sd05Sd0 or 1030(56) (Figs. 28 and 29). Other shells have broader bands with the notation 10(34)(56) (Figs. 26 and 27). A few specimens from S. Vicente and Sal have the central coloured area expanding anteriorly: 10(34)Sd50 (Fig. 30 and 31). The bands may in some cases be very pale or even absent, mainly in Boavista specimens (notation 000000).

Live animal   The animal (Fig. 44) was observed on Sal, S. Vicente and Boavista (PEICV), and on Santiago and Brava (E. Rolán pers. comm). It is pigmented on the whole dorsal side of the foot, tentacles and siphon, with small black dots, mixed with brown and white dots. The white flecks are concentrated on the anterior and posterior parts. The mantle edge has elongated black spots, alternating with white ones. The surface of the mantle is slightly rugose, with black, brown and white spots; the inner part of the mantle is visible through the shell and has irregular dark areas on a pale background.

Radula   The radular teeth always have a central very high cusp with a smooth base. There are differences in teeth between island groups (Tab. 2). In Sal-Boavista they are smaller (the shells also) but have more cusps (8 on each side) (Fig. 50). In S. Vicente-S. Luzia they are large with few cusps, less than 6 on average on each side of the central cusp (Fig. 51). On the latter, the central cusp has a very broad smooth base and the lateral cusps are well developed.

Geographic range and Habitat   This species has been found on all islands (Map 5). It is very frequent on Sal, S. Vicente, S. Luzia, and Boavista in shallow depths of the infralittoral, from a few centimetres to a few metres (1–20) in areas of stones surrounded by sand.
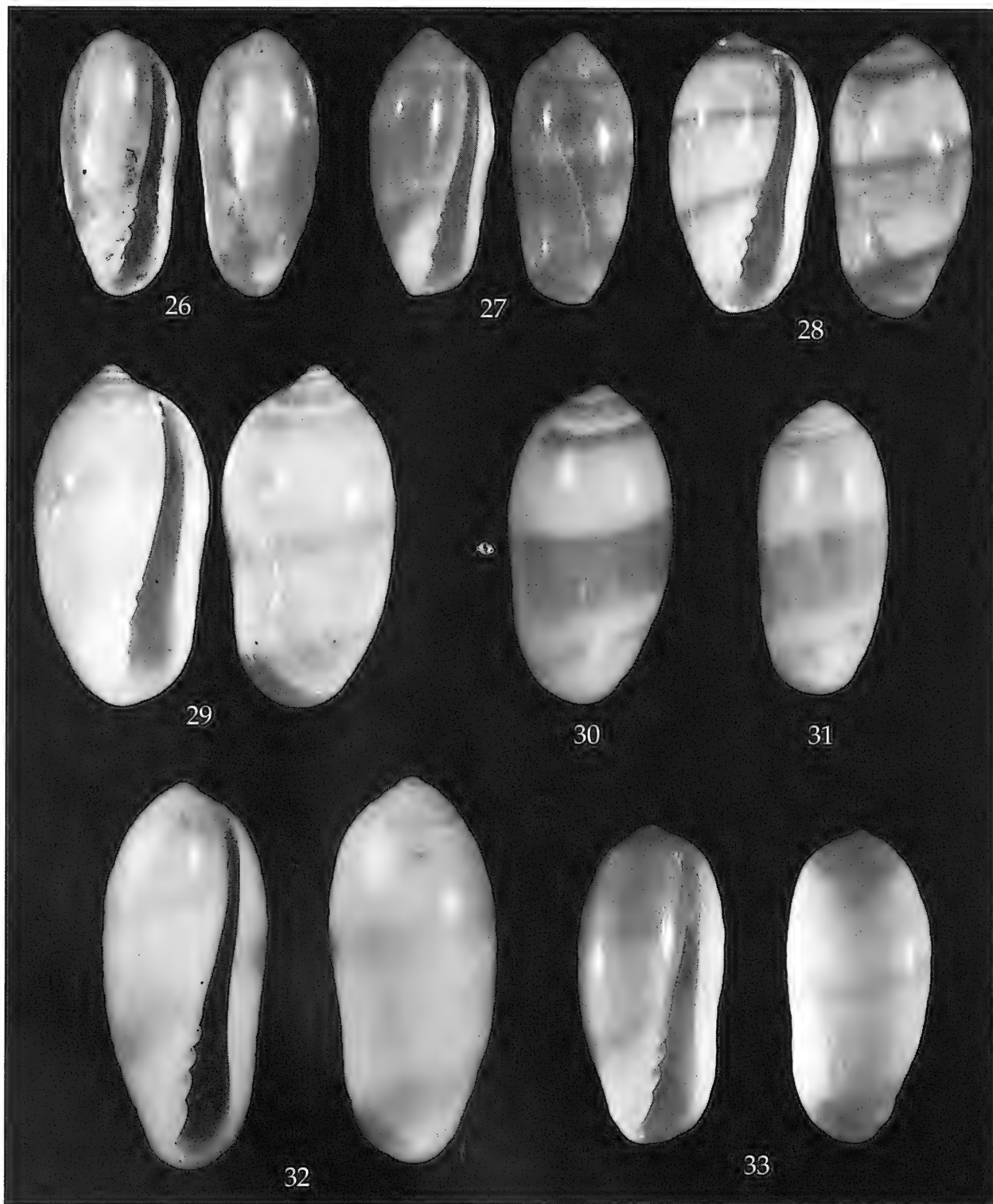
Figs 26–31 *Volvarina cernita* (Locard, 1897): **26** *V. cernita,* syntype, –20 m dredging S. Vicente (MNHN) (5.1 x 2.4 mm), S–10(34)(56). **27** *V. cernita:* Palmeira, Sal (PEICV) (7.1 x 3.4 mm), S– 10(34)(56). **28** *V. cernita:* Saragasa, S. Vicente (PEICV) (7.4 x 4.0 mm), S–103050. **29** *V. cernita:* Curral, S. Luzia (ER) (9.0 x 4.7 mm), S–1030(56). **30** *V. cernita:* Saragasa, S. Vicente (PEICV) (8.1 x 4.1 mm), P–10(34)Sd50. **31** *V. cernita:* Guincho do Ninho, Sal (PEICV) (6.7 x 3.4 mm), S– 10(34)Sd50. **Figs 32–33** *Volvarina nuriae* n. sp.: **32** *V. nuriae* n. sp., holotype, Sal Rei, Boavista (PEICV) (10.5 x 4.7 mm), P–10(23)0(56). **33** *V. nuriae* n. sp.: paratype 3, Sal Rei, Boavista (PEICV) (9.7 x 4.6 mm), S– 1030(56).

Comparisons and Remarks   There are important shell differences between islands, particularly between Sal–Boavista and the S. Vicente-S. Luzia island complex. The shells from Sal–Boavista are usually smaller, more slender, and have a more diffuse colour pattern.

Those from S. Vicente–S. Luzia are usually comparatively large and broad, with narrow, sharp colour bands, but not always.

The main difference with the other studied species (except *V. sauliae*), is that the shell is broader (the L/Ws ratio is usually under 2) (Fig. 46).

This species is difficult to understand because of its variability and unclear type. The syntype of *V. cernita* (Fig. 26) is a very small specimen (5.1 mm long). The smallest adult in our material is 5.8 mm long (S. Luzia). *V. cernita* was described with a rather peculiar pattern of three dark bands, the central one broader and separated from the anterior dark band by a narrow, unpigmented band. This is not the pattern that we have most commonly found, but similar banding was seen in our material (Fig. 27). The pattern of *V. corallina* is also similar, but the central band is broader and the colour more intense (brown). In these circumstances, the colour pattern of living animals is decisive to separate the species.

In the typical pattern of this species there are three pigmented areas with a narrow central band. This pattern is similar to that of *V. nuriae* n. sp., and *V. sauliae*. *V. nuriae* n. sp. have a more slender shell and two well defined tones (pink or straw), while *V. cernita* does not clearly have two alternative colour morphs (it is usually straw-coloured). A few specimens, particularly among the large ones from S. Vicente or S. Luzia, have pinkish tones on the colour marks of the outer lip. A single specimen with pinkish bands was seen (Fig. 30). The shell of *V. sauliae* is always broader than that of *V. cernita*.

Shell size of *V. cernita* is always smaller than that of *V. taeniata*, a sympatric species with a different pigmented pattern (four bands). *V. cernita* is usually smaller than *V. boyeri* n. sp. and *V. verdensis*, both sympatric with it. The shell pigmentation pattern of these species is different, having usually four or six bands. In *V. cernita* there are a few specimens with colourless shells. This pattern was never seen in other species.

The animal was briefly described by Burnay & Monteiro (1977, as *Marginella* sp.), see also Coovert (1987, as *Volvarina* sp.), and figured by Boyer (1998, photograph as *Volvarina* sp. 1). Observations of living animals in specimens from several islands were very helpful to assimilate forms with quite a distinct shell appearance. The pattern is similar to that of *V. verdensis*, but differs in having more black dots than brown ones, contrary to the latter species. The size and shell band pattern of both species are always different.

The central cusp of the radular teeth is, proportionally, the highest of all the species examined here. In S. Vicente–S. Lucia specimens, the shell length/tooth width ratio (L/Wr) is the smallest (24.86), showing a relatively large radula, and the number of lateral cusps the smallest among all the species studied. The central cusp has a peculiar base (broad and lacking lateral cusps) different from that of all other Cape Verde Islands species, but curiously similar to that of *V. obscura* from the Red Sea.

The name *V. tribalteata* (Reeve, 1865), used by Jousseaume (1877) for a Cape Verde Islands species, is a synonym of *V. exilis* (Gmelin, 1791) (Gofas, 1989), a species from Senegal. The name *V. exilis* was also used for a CapeVerdian species by Knudsen (1956) and Cosel (1982). *V. exilis* differs from *V. cernita* in its larger size and the three colour bands on the body whorl that are vague and do not extend onto the outer lip.

The name *V. mitrella* (Risso, 1826) was used by Saunders (1977) for a Cape Verde Islands species. *V. mitrella* is a Mediterranean species (Muñiz Solis, 1987; Gofas, 1989) (1977) and differs from V. *cernita* in the shell form, with a globular apex, in the shell pigmentation, usually with a uniform pale brown colour, and in the radular teeth, lacking a prominent central cusp.

V. insulana Gofas & Fernandes, 1988, from S. Tomé and Principe, is similar to *V. cernita* in size and conchological characters, but the former is distinguished by its shape, which is regularly fusiform. The pattern of the living animal of *V. cernita* is similar to that of *V. insulana*, but differs in having more black dots than brown ones, contrary to the latter

species. The radular teeth of both species are similar, but in *V. insulana* there are more cusps on each side of the central cusp (8–10) (Fernandes & Rolan, 1991; Gofas & Fernandes, 1992). Also, in *V. cernita* the central cusp is larger than that of *V. insulana*.

V. oceanica Gofas, 1989, from Azores, is similar in size and conchological characters to *V. cernita*, but it is distinguished by having the three brown bands of the body whorl broader than in *V. cernita*.

V. peregrina Gofas & Fernandes, 1992, from Angola, is similar in size, conchological characters and colour pattern of the living animal, but differs in having the three brown bands of the body whorl broader than in *V. cernita*.

<div align="center">

***Volvarina nuriae* n. sp.**
Figs. 32–33, 45, 52–53, Map 6

</div>

Volvarina sp. CV— Coovert & Coovert, 1990: 40, Fig. 92 (radula).

Holotype   1sp collected by the authors (PEICV, UAM no. 230), 26th August, 1985, from Baia de Sal-Rei (west), Boavista, in MNCN (no. 15.05/27466) (includes radula).

Paratypes   7 sp (paratypes 1–7) as holotype, in MNCN (no. 15.05/27466), MNHN and BMNH; 3sp (paratypes 8–10) collected by the authors (PEICV, UAM no. 255), 25th August, 1985, from Baia de Sal-Rei (north), Boavista, in ER and DM.

Type locality   Baia Sal Rei, Boavista, Cape Verde Islands, 1–2 m.

Other material examined   **Boavista** 3 sh + 1 sh, no locality (ER, FF). 27 sp + 16 sh + 3 sp + 1 sh, Baia Sal-Rei (UAM, IIT, EM2, FF).

Measurements (mm)

	Length (L)	Width (Ws)	L/Ws	Colour	Radula (included)	Figure	Collection
Holotype	10.2	4.5	2.26	pink	yes	32	MNCN
Paratype 1	9.4	4.2	2.24	pink	no	——	MNCN
Paratype 2	9.5	4.1	2.32	straw	no	——	MNCN
Paratype 3	9.6	4.4	2.18	straw	yes	33	MNCN
Paratype 4	9.1	4.2	2.17	pink	no	——	MNHN
Paratype 5	9.1	4.0	2.27	straw	yes	——	MNHN
Paratype 6	9.4	4.2	2.24	straw	no	——	BMNH
Paratype 7	8.9	4.0	2.22	pink	no	——	BMNH
Paratype 8	8.8	3.9	2.26	pink	no	——	ER
Paratype 9	8.9	4.0	2.22	pink	teratological	53	DM
Paratype 10	9.6	4.5	2.13	pink	yes	52	DM

Description   The shell size shows little variation (see above, Table 1 and Fig. 46). It has 3.5–4 whorls and is elegantly ovate-cylindrical. The thickening of the outer lip is marked by a very weak external varix, is whitish and shows the termination of the pigmented bands. There are four columellar plications and a very weak longitudinal callus. The shell is somewhat translucent, and the animal is visible through it.

The shell pigmentation is always pink or straw–coloured; the most frequent (²⁄₃) being the pink morph. There are three spiral coloured areas on a pale, whitish unpigmented background; the anterior is close to the siphonal notch, the median is narrow

and quite exactly in the middle, the posterior next to the suture. The pale zones separating the bands are broader than these and of equal width. The species shows little variation in banding pattern, only in the intensity and breadth of the median band. The typical notation is: 1(23)0(56) or 1030(56), always with narrow unions (Figs. 32 and 33).

Live animal   The dominant colour of the animal is somewhat orange in animals with a pink shell, and brown in animals with a straw–colored shell. The dorsal part of the foot is not pigmented, as only the anterior edge has tiny scattered dots. The siphon has coloured dots (orange or brown), which may form a diffuse blotch, concentrated towards the distal end. The tentacles have coloured spots (orange or brown) alternating with white dots. The inner part of the eyes is bordered by a semicircular coloured mark (orange or brown) resembling "eyebrows". The surface of the outer mantle was not observed; its edge is unpigmented. The inner part of the mantle is visible through the shell, but apparently is unpigmented.

Radula   The teeth are broad and the central cusp does not protrude very much, having a smooth base (Fig. 52 and Tab. 2). There are more than 10 lateral cusps on each side (average). We found one teratological radula, with the central cusp smaller than the others throughout (Fig. 53). See also Coovert & Coovert (1990: 40).

Derivation of name   The species is dedicated to **Nuria** Martín Herrero, wife of the first author, as a tribute to her constant help and patience.

Geographic range and Habitat   This species was found only on Boavista in the area of Baia de Sal-Rei (Map 6), where it is very abundant at shallow depths, from a few centimetres to 2 metres. It lives in rocky areas with plenty of sand nearby. The bay of Sal-Rei is essentially sandy, with long stretches of beach.

Comparisons and Remarks   *V. nuriae* n. sp. is different from all the other studied species in its pigmentation pattern (shell and animal). The shell has very characteristic pigmentation with three well defined bands. The animal has a coloured "eyebrow", unique to this species.

   V. nuriae n. sp. differs from *V. taeniata* in size (always smaller), in shell pigmentation pattern (only three colour bands), and in animal pigmentation pattern (dorsal part of the foot unpigmented).

   The size of *V. nuriae* n. sp. is similar to that of *V. verdensis* from which it is distinguished by the outline (more elongated) and, overall, the shell pigmentation (always with three narrow bands) and animal pigmentation (lacking dark dots). In *V. nuriae* n. sp. pink morphs are the most frequent, contrary to *V. verdensis* and *V. taeniata*. The radula has fewer cusps than *V. verdensis*, the sympatric species of more or less the same size.

   V. nuriae n. sp. and *V. cernita* have a very similar banding pattern on the shell, but the bands are broader and more stable in the former. The two species can be separated by their dimensions and L/Ws ratio (*V. nuriae* n. sp. is more slender) and by the animal pigmentation pattern (*V. cernita* has dark spots).

   V. nuriae n. sp. differs from *V. mediocincta* in size (always larger), in shell pigmentation (three colour bands), and animal pigmentation pattern (*V. nuriae* n. sp. has the dorsal part of the foot unpigmented while *V. mediocincta* has some large orange spots).

   V. nuriae n. sp. is very different from *V. sauliae* in size (always larger), L/Ws ratio (shell more elongated), and radular features (teeth always larger, and the central cusp with a smooth base).

   V. joubini Dautzenberg & Fischer, 1906 (not Bavay, 1910) is similar in size and proportions to *V. nuriae* n. sp. The shell of *V. joubini* is more conical and narrower towards the

siphonal canal, whereas in *V. nuriae* n. sp. is more cylindrical. In apical view, the last whorl of *V. joubini* is straight and almost perpendicular to the surface of the preceding whorl, whereas in *V. nuriae* n. sp. this edge is concave. The main difference is in the colour pattern. The type of *V. joubini* (quoting the original description as the specimen has now lost all colour) has three straw-coloured bands, the median one rather broad, alternating with two pale bands of which the anterior one is narrower. In *V. nuriae* n. sp. the pale bands are broad and of equal breadth, and the central band is consistantly narrow, the only variation being the alternate straw/pink colour. *V. joubini* is a probable circalittoral species.

The radular teeth are similar to that of *V. verdensis*, but smaller and with fewer cusps (10.5\11 on each side) (Fig. 52). Coovert & Coovert (1990: 40, Fig. 92) studied and figured the radula of this species as "*Volvarina* sp. CV" (det. fide G. Coovert, pers. comm.); their data fit our observations.

V. nuriae n. sp. is different from mainland species of *Volvarina* in the three colour bands on the body whorl that extend onto the outer lip (see Comparisons and Remarks of *V. cernita*).

V. insulana Gofas & Fernandes, 1988, from S. Tomé and Principe, is similar in size and conchological characters. This species is distinguished by the colour pattern of the shell, with three fading bands on the body whorl, by the living animal, with several dark spots on the foot, and by the radular teeth, with lateral cusps near the central one.

V. oceanica Gofas, 1989, from Azores and *V. peregrina* Gofas & Fernandes, 1992, from Angola, are similar in conchological characters to *V. nuriae*, but they are smaller and the three brown bands of the body whorl are broader than in *V. nuriae*. The living animal of *V. peregrina* differs from that of *V. nuriae* in the foot pattern "covered with orange, yellow and black spots" (Gofas & Fernandes, 1992).

Volvarina joubini (Dautzenberg & Fischer, 1906)
Fig. 34, Map 6

Marginella (Volvarina) joubini Dautzenberg & Fischer, 1906 (non Bavay, 1910): 18, Pl. 1, Fig. 17 (no locality given)
Marginella (Volvarina) joubini Dautzenberg & Fischer, 1906— Tomlin, 1917: 273 (Loc. not given).

Type material   Marginella (Volvarina) joubini: 1 syntype, MOM (Fig. 34) (the label reads Sta. 1203, which is 15°54′N, 22°54′45″W, 91 m, 4 miles SW of Boavista).

*Description   * Shell dimensions (syntype) are shown in Tab. 1 and Fig. 46. The shell has 4.0 whorls and is elongate-cylindrical, tapering anteriorly. The outer lip is thickened, lacking an external varix. There are four columellar plications and a weak longitudinal callus, just posterior to the plications.

The shell pigmentation (rewritten from the original description) comprises three straw-coloured bands, the median one rather broad, alternating with two pale bands of which the anterior is narrower. The colour pattern is darker when overrunning the outer lip. The syntype lost colour and it is now impossible to assign a notation.

*Live animal   * The pigmentation of the animal is unknown.

*Radula   * There are no data.

*Geographic range and Habitat   * The species is known only from the syntype for which no locality is given in the original publication, neither in the text nor in the appendix. This is surprising as details of stations are given by Dautzenberg & Fischer (1906) for all other

species, and may cast some doubt on the origin of the specimen. The label of the syntype reads Sta. 1203, the location of which is given in the Map 6. The most likely, however, is that it is a circalittoral species and so is not represented in our material.

Figs 34 *Volvarina joubini* (Dautzenberg & Fischer, 1906), syntype, Boavista –91 m dredging (MOM) (8.3 x 3.9 mm).
Figs 35–37 *Volvarina sauliae* (Sowerby, 1846): **35** *V. sauliae,* neotype, Prainha, Praia, Santiago (BMNH, from ER) (6.8 x 4.1 mm), S–103050. **36** *V. sauliae:* Pesqueiro do Aire, Sal (PEICV) (7.6 x 4.6 mm), S–103050. **37** *V. sauliae:* Baia Pedrinha, Brava (ER) (8.3 x 4.7 mm), S–103050.
Figs 38–39 *Volvarina obscura* (Reeve, 1865): **38** *Volvarina obscura,* holotype, Aden ?, Red Sea (BMNH) (8.7 x 4.2 mm). **39** *V. obscura:* Red Sea (MNHN) (11.7 x 5.6 mm and 10.7 x 5.1 mm), S–12345.

Comparisons and Remarks   This likely circalittoral species presents some features different from all the littoral species: the longitudinal callus just posterior to the plications is more developed and the shell lacks an external varix.

The *V. joubini* pattern described is reminiscent of *V. cernita* and *V. corallina,* but shape and shell measurements do not agree with them. The specimen has now lost all pattern and has a dull, colourless appearance.

Size is similar to *V. nuriae,* but there are differences in shell form and colour pattern. The type of *V. joubini* (quoting the original description as the specimen has now lost all colour) has three straw-coloured bands, the median one rather broad, while in *V. nuriae* n. sp. the central band is consistantly narrow (see Comparisons and Remarks regarding *V. nuriae* n. sp.).

Volvarina sauliae (Sowerby, 1846)
Figs. 35–37, 54, Map 7

Marginella sauliae Sowerby, 1846b: 368, Pl. LXXV, Fig. 68 (unknown locality).
Gibberula jousseaumi Rochebrune, 1881a: 30 (Porto Praia).
Marginella sauliae Sowerby— Chenu, 1859: 197, Fig. 1038.
Egouena sauliae Sowerby— Jousseaume, 1875: 33; 1877: 270 (Cape Verde Is.).
Gibberula jousseaumi Rochebrune— Rochebrune, 1881b: 293, Pl. 17, Figs 15 a and b (Porto Praia; S. Vincente).
Gibberula jousseaumi Rochebrune— Tomlin, 1917: 273 (Porto Praia, S. Vicente).
Marginella jousseaumei Rochebrune, 1881 (not Locard, 1897)— Marche-Marchad, 1956: 57 (Cape Verde Is.).
Marginella jousseaumi Rochebrune— Burnay and Monteiro, 1977: 44, Fig. 43 (Sal).
Gibberula jousseaumi Rochebrune— Cosel, 1982a: 20 (Sal); 1982c: 57 (Cape Verde Is. endemic).
*Volvarina sauliae* (Sowerby, 1846)—Gofas & Fernandes, 1992: 192.

Type material   *Marginella sauliae:* Type not found in BMNH. One specimen measuring 6.8 x 4.1 mm (Fig. 35), from Praia, Santiago, Cape Verde Is. (ER), is designated here as neotype (BMNH, No. 1998083). *Gibberula jousseaumi:* Type not found in MNHN

Other material examined   **Boavista** 3 sh, Sal Rei and Baia Teodora (FF). **Brava** 3 sp, Baia Pedrinha (ER). **Sal** 9 sh, Algodoeiro (MNHN). 1 sh, Pesqueiro do Aire (UAM). 3 sh, Palmeira (ER). 1 sh, S. Maria (ER). 4 sh, Parda (MNHN). 8 sh, Baia Cerro Negro (MNHN). 6 sh, Mordeira (MNHN). **Santiago** 1 sh, Praia (ER).

Description   Shell dimensions are given in Table 1 and Fig. 46. Specimens from Brava are somewhat larger and more slender. The shell has 4–4.25 whorls and is ovate-triangular with the broadest part quite close to the suture of the body whorl. The edge of the outer lip is thickened, with a weak external varix, and shows the termination of the coloured bands.There are four well developed columellar plications and a very weak longitudinal callus (not always visible), just posterior to the plications. The shell is somewhat translucent and the inner mantle is visible.

There are three narrow bands of straw colour, the most intense band runs along the suture and is readily seen on the spire whorls. The other two bands, one median (paler) and the other anterior, close to the siphon, are sometimes hardly visible on the surface of the body whorl, but are always detectable on the thickened part of the outer lip. The notation is always: 103050 (Figs. 35–37) or 103050. In specimens from Brava, the area between the central and anterior band is often slightly tinged with pink (Fig. 37).
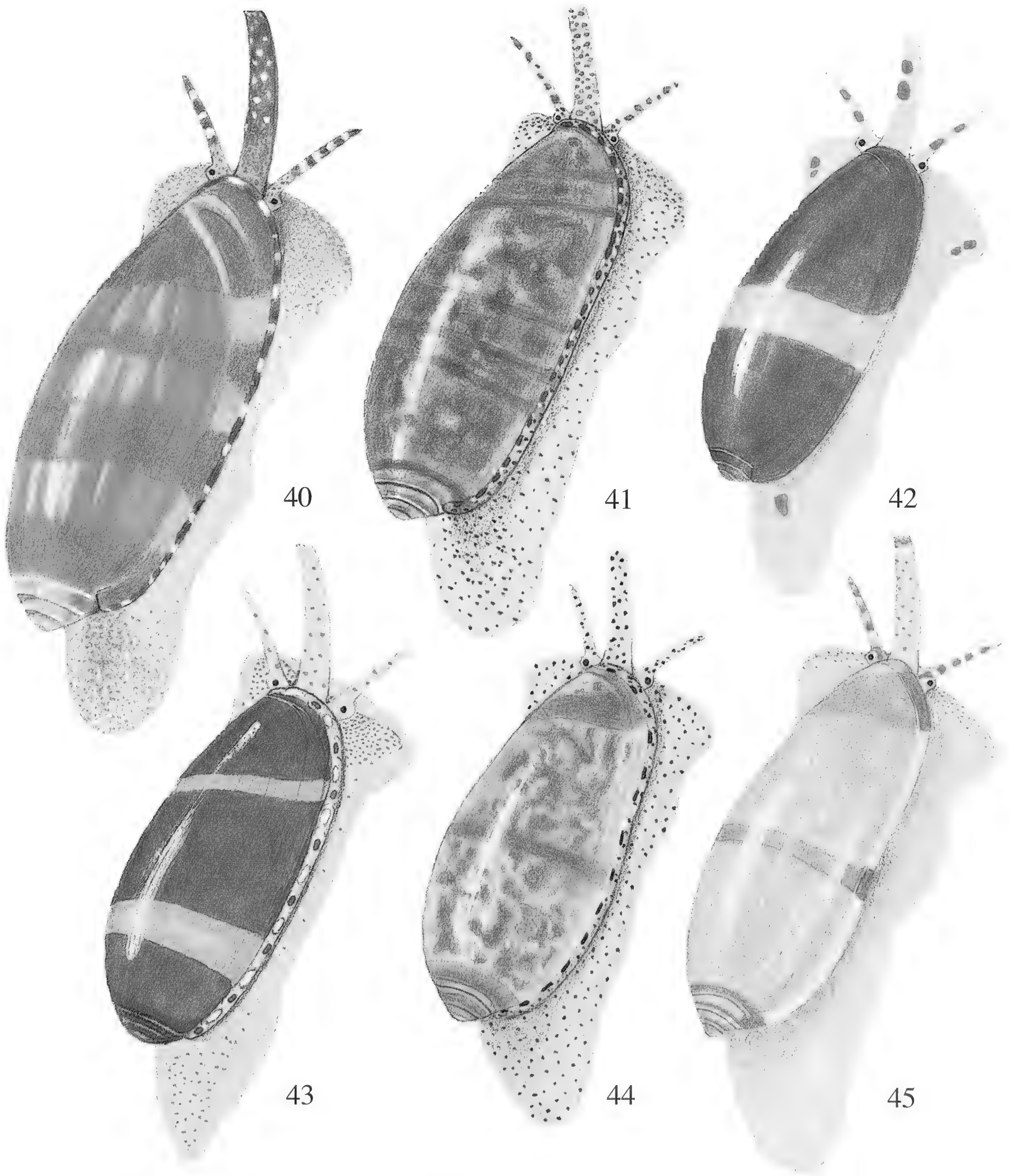
Figs 40–45 Live animals of *Volvarina* (shell length in brackets). **40** *V. taeniata* (Sowerby, 1846): Joaquim Petinha, Sal (13.7 mm). **41** *V. verdensis* (E.A. Smith, 1875): Sal Rei, Boavista (10.0 mm). **42** *V. mediocincta* (E.A. Smith, 1875): Rigona, Sal (6.1 mm). **43** *V. corallina* (Bavay, 1910): Ponta Geneanes, Santiago (6.7 mm). **44** *V. cernita* (Locard, 1897): Palmeira, Sal (7.1 mm). **45** *V. nuriae* n. sp.: Sal Rei, Boavista (9.0 mm).

Live animal   The morphology and pigmentation of the animal are unknown.

Radula   The radula (Table 2 and Fig 54) is small (W= 146 µm) (L/Wr= 54.73). Each tooth has a well-developed central cusp and 9.6\10.0 lateral cusps on each side of it (mean). The lateral cusps are poorly developed and reach the base of the central cusp.

Geographic range and Habitat   This species was collected on four islands: Sal, Boavista, Santiago and Brava (Map 7). It is likely to exist on the other islands, since Sal and Brava are the farthest apart in the archipelago, with the other islands in between. Rochebrune (1881a), shows as type locality "Porto– Praya" (Santiago) in the description of *Gibberula jousseaumi*, but extends its range to "Porto–Praya and Saint–Vincent" in his next paper (Rochebrune, 1881b). However, specimens from S. Vicente are not present in our material despite numerous samples, or in the material studied from several museums. Therefore, the locality S. Vicente is uncertain. On Brava it lives in shallow waters in sandy bottoms (1–2 m, E. Rolán pers. comm.), the shells are more slender and larger and the population is possibly the most isolated. On Sal it was always found in small numbers and as dead shells, and is likely to live in the first few metres of water near shore.

Comparisons and Remarks   The shell is very distinct from any of the other Cape Verdian species of *Volvarina*, and superficially resembles a *Gibberula*. We consider the species a member of the genus *Volvarina* due to its radular features, Type 6 with a prominent central cusp, and shell features, with a very weak external varix and a pigmentation with blotches on the outer lip (continuation of the coloured bands), that are very similar to that of all other Cape Verde species of *Volvarina*. Coovert & Coovert (1990) used the name *Prunum* cf. *sauliae* (Sowerby, 1846) (see also Kaicher, 1973: card no.25) for two specimens from Cape Verde (Senegal) and Gabon, respectively, and studied their radulae. These radular teeth lack a prominent central cusp and probably belong to other species (shell length 11.3 mm and 10.8, respectively).

   Among all the Cape Verde species, *V. sauliae* has by far the lowest L/Ws ratio (1.78–1.60) and, therefore, the broadest shell. The body whorl covers most of the preceding ones, yet not as much as in the other species. Specimens from Brava are somewhat larger and more slender. The columellar plications are more developed than in other species.

   The shell pigmentation pattern is similar to that of *V. cernita*, but in the latter it is more variable, and usually with broader bands. *V. sauliae* is always distinguished by its broader shell.

   V. riparia Gofas & Fernandes, 1992, from Angola, is similar in shape and size, but differs in the outer lip lacking colour, and in the radular characters (see Gofas & Fernandes, 1992: 192, for comparison with *V. sauliae*).

   All of the mainland West African *Volvarina* lack the colour blotches on the lip, which are distinctive in *V. sauliae*. *V. exilis* (Gmelin, 1791) further differs by completely lacking an external varix (see Gofas, 1989: 173–176 for further discussion). Most of the mainland West African *Volvarina* lack the subsutural brown band, another distinctive feature of *V. sauliae*. The only species with a distinct subsutural brown band is a species from Senegal identified by G.A. Coovert (pers. comm.) as *V. annulatum* (Reeve, 1865) (see Kaicher, 1981, card 2666). It differs in lacking the lip blotches and in having the anterior two columellar plications fused together outside of aperture, forming a thick, raised mass.

   Regarding the radular features, the shell length/tooth width ratio (L/Wr= 54.73) is larger than that of all the other species studied, showing a relatively small radula. The base of the central cusp, with small lateral cusps, is also different among the Cape Verde Island species, except *V. verdensis*.

V. sauliae was described from an unknown origin and the type locality of *V. jousseaumi* is Porto Praia on Santiago (see above). Sowerby (1846b), in the original description of *V. sauliae*, mentions a shell with two coloured bands "lineis rubris binis cincta", but the figure shows a dark line along the suture, too. The figure shows the anterior line close to the central one, whereas on our material it is closer to the siphon, but the lines are continued over the outer lip, terminating with a more intense blotch thereon, as in our material and in all *Volvarina* species from the Cape Verde Islands. Chenu (1859) shows a figure also with three bands. Jousseaume (1875, 1877) was the first to attribute *V. sauliae* (as *Egouena sauliae*) to the Cape Verde Islands.

In accordance with ICZN Art. 75, we have found it necessary to stabilize the nomenclature of *Volvarina sauliae* by designating a neotype, as no type material is now believed to exist. We consider the closely similar mainland species, and previous reference to them as *V. sauliae*, to constitute "exceptional circumstances". The presence of the colour blotches on the lip of *V. sauliae* serves to distinguish this species from all mainland West African species. This feature is clearly shown in Sowerby's original figure. The specimen selected as neotype (Fig. 35), from Santiago (ER), is very similar to the original description and figure, and has been deposited in the BMNH (see type material). Further differentiation from Cape Verde Islands species as well as other mainland species is discussed above. Because of the distinctive colour blotches on the lip, plus shape and size, Sowerby's species is most certainly the same as the neotype.

As regards the status of the type of *V. sauliae*, Tomlin (1917) quoted "There is now no trace of this shell in the Saul collection (fide H. Scott)". According to K. Way (BMHN, pers. comm.) "*Marginella sauliae* was described from the Saul collection, which is housed in the University Museum, Cambridge". However, she did not find this material in her paper on the types in the Saul collection (Bishop & Way, 1976). It thus appears that the type of *V. sauliae* is permanently lost or destroyed.

The original description and figure of *Gibberula jousseaumi* agree with *V. sauliae* and we consider it to be a subjective synonym. The dimensions given by Rochebrune fit our observations for *V. sauliae* although towards the lower interval (6 x 4 mm). We examined two specimens in the MNHN Jousseaume collection, one without the original label but separated as a possible syntype of *V. jousseaumi*, and one labeled "*M. sauliae* Sow./*M. jousseaumi* Rochebrune/Cap Vert". Both are small, slender specimens which we refer to as *Volvarina cernita*. There is such discrepancy with the measurements (7.1 x 3.7 mm and 6.0 x 3.0 mm) and with the original figure that some subsequent mixing has obviously occurred and these are not types. Rochebrune (1881b) included *V. sauliae* and *Gibberula jousseaumi* in his paper. He probably believed that *V. sauliae* was a typical and slender Cape Verde Island *Volvarina* (it had been cited in the Cape Verde Islands by Jousseaume (1875, 1877)) and described the broad species as a *Gibberula*.

Volvarina obscura (Reeve, 1865)
Figs. 38–39, 55

Marginella obscura Reeve, 1865: Pl. 24, Fig. 132 (Aden ?).
Marginella obscura Reeve— Tomlin, 1917: 284 (unknown locality, Mus. Taylor).
Volvarina obscura (Reeve)— Kaicher, 1992: card 2686/6191 (Aden).

Type material   Marginella obscura: Lectotype, designated by Tomlin (1917: 284, as "Type.– Brit. Mus., on same tablet as three from Aden (Yerbury)"), BMNH no. 1874.12.11.80, marked with an "x" on a tablet for 4 specimens. Three other specimens (paralectotypes) BMNH no. 1888.4.9.146; no. 1896.4.9 146; no. 1896.5.6.107.8.

A specimen of *Volvarina obscura* of the BMNH type collection (not the lectotype) was figured by Kaicher (1992: card 2686/6191).

Other material examined   No locality 1 sh (MNHN, Coll. Jousseaume). **Red Sea** 27 sp, no locality (MNHN, Coll. Jousseaume). 19 sp, Aden (MNHN, Coll. Jousseaume). 14 sp, Obock, Djibouti (MNHN, Mission Ch. Gravier, 1904).

Description   The shell length averages 9.6 mm (Table 1). The shell is ovate-cylindrical, with the body whorl covering all the others and almost reaching up to the apex in adults. The thickening of the outer lip is slight, with a weak external varix, and shows the termination of the coloured bands. The somewhat translucent shell has four columellar plications.

The shell pigmentation is composed of 5 straw-yellow spiral bands on a pale background. The posterior band is along the suture and the anterior one is very close to the siphon. The other three bands are equal and equidistant. The bands are clearly marked over the thickened outer lip. The notation, based on only 5 bands, is always 12345 (Fig. 39).

Live animal   The animal and its pigmentation are unknown.

Radula   The radular teeth are on average 355 µm wide (Wr) and have a prominent sloping central cusp with a smooth base. There are 7-7.5 cusps on each side (Tab. 2 and Fig. 55), and the impressions of the cusps of the neighbouring tooth are visible.

Geographic range and Habitat   This species is known from a small area in the Southern Red Sea and the Gulf of Aden on the coast of Aden and Djibouti (Obock). There are no data on its habitat, but from the numerous lots of live-collected specimens in the Jousseaume collection (MNHN) it is supposed that it lives in the upper part of the infralittoral.

Comparisons and Remarks   This species is very similar in size and general appearance to the Cape Verde Islands species and was confused with them by Cosel (1982a, c). Three lots from Aden, Red Sea and Djibouti (MNHN, Jousseaume collection) were labeled *V. taeniata*, which is incorrect (*V. taeniata* is a Cape Verde Islands endemic). Nevertheless, in *V. obscura* the shell pigmentation is unmistakable and makes a pattern with 5 bands, which is not found in Cape Verde Islands species, with patterns derived (by fused or missing bands) from a basic six-band plan. In Cape Verde Islands species the second band is far from the first, while in *V. obscura* it is close. In *V. taeniata*, bands 5 and 6 are always fused to form a broad zone, and there is never a narrow fifth band. The pattern of *V. obscura* has five equal and equidistant bands. It is therefore not comparable with Cape Verde Islands species. *V. obscura* does not have the alternative pink colour as do most of the species from the Cape Verde archipelago. The body whorl also covers more of the spire than in Cape Verde Islands species.

A *V. obscura* specimen from the Indian Ocean was figured by Kaicher (1981: card 2686). Kaicher (1992: card 2686/6191) figured another specimen of *V. obscura* from Aden (BMNH type collection) and stated that the former is not conspecific.

Strangely, the radular teeth of *V. obscura* are very similar to those of the Cape Verde species, above all *V. cernita* from S. Vicente–S. Luzia.

Coan & Roth (1976: 220) described the radular tooth of *V. obscura* (from unknown locality) as "Comblike rachidian plates bearing 14 cusps". The radular teeth of four specimens of *V. obscura* of authors from Oman and SE Arabian were studied and figured by Coovert & Coovert (1990: 52–53, Figs. 120–123). Those specimens are larger (16 mm shell length) than our study specimens (maximum 11.7 mm and average 9.6 mm) and surely belong to another species. However, the curved central cusp is very similar.

A sinistral specimen of the same species was quoted by Coovert & Lee (1989: 9) from Oman (12.6 mm shell length).

Discussion

Shell measurements show significant differences in size among the species of the Cape Verde Islands radiation of *Volvarina* (Tab. 1). Except for the very different *V. sauliae*, the species *V. taeniata*, *V. verdensis*, *V. cernita* and *V. mediocincta*, all of them sympatric on several islands, have decreasing size ranges with slight overlaps (Fig. 46). There are some exceptions. *V. nuriae* n. sp. is equivalent in size to *V. verdensis* (both sympatric on Boavista), but more slender. *V. boyeri* n. sp., is equivalent in size to *V. verdensis* and *V. nuriae*, but the former is a Sal endemic, while the other species have allopatric distribution. *V. mediocincta* is equivalent in size to *V. corallina*, and both are sympatric at least on Brava. The L/Ws ratio in *V. cernita* and *V. sauliae* is smaller than in other species. In relation to the size, *V. obscura*, from the Red Sea, is intermediate between *V. taeniata* and *V. verdensis*, both from the Cape Verde Islands. There are always four columellar plications, which are more developed in *V. sauliae*, and a weak longitudinal callus just posterior to the plications, is more developed in *V. joubini*.

The most extreme variability in banding is seen in *V. verdensis* with a maximum of six bands. In some cases, the geographic origin of the specimens can be inferred from the colour patterns (e.g. *V. verdensis* from Maio or the east coast of Santiago).

V. taeniata, a variable species, has a maximum of four pigmented bands, while *V. boyeri* n. sp. always has four equal coloured bands. There are only three pigmented areas or bands in *V. corallina*, *V. cernita*, *V. nuriae* n. sp., and *V. sauliae*. *V. cernita* has the highest variability with more or less broad bands. *V. mediocincta* stands apart with its characteristic two broad dark zones separated by a pale central area.

Some specimens of *V. verdensis* from Fogo show the complete union of bands, while some specimens of *V. cernita*, mainly from Boavista, are colourless.

In the species *V. taeniata*, *V. verdensis*, and *V. nuriae* n. sp. colour morphs with either pink or straw colour bands exist within the same population. In *V. verdensis* and *V. taeniata*, the straw colour is the most frequent, comprising approximately ⅔ of the study specimens. The opposite is seen in *V. nuriae* n. sp. in which the pink morphs are approximately ⅔. *V. cernita* and *V. sauliae* have variable tones of straw colour, rarely with pink tones. Other species have only one colour: *V. boyeri* (purplish–pink), *V. mediocincta* (brown, more or less dark), and *V. corallina* (reddish–brown).

V. obscura has a different pattern from those of the Cape Verde species, with five equal and equidistant bands, and is always straw–coloured.

The colour patterns of the living animals have been very helpful to separate and define seven of the species, and were essential when convergent banding patterns occurred with the shells. Although there is some variability between populations from different islands, it is much less than the conchological variation and proves to be a stable character.

There are few data on the surface of the outer mantle because it covers the shell almost completely only when the animal is undisturbed. The surface is slightly rugose at least in the largest species, *V. taeniata*, and in *V. cernita*.

The radular teeth were studied in several species of *Volvarina* by Coovert & Coovert (1990), including two species from Cape Verde Islands, *V. verdensis* and *V. nuriae* n. sp. (as "*Volvarina* sp. CV"). Their data and ratios on Cape Verdian species fit our observations (Tab. 2). All the studied species in the present paper, including *V. obscura* from the Red Sea, have a Type 6 radula with comb-like teeth and a central cusp larger than the others. All the radulae are very similar, but there are some small details that differ between species (Tab. 2 and Figs. 47–55).

The number of cusps overlaps between species, ranging from over 12 on each side of the central cusp in *V. verdensis* to 5.6 in *V. cernita* from S. Vicente. *V. cernita* is again the most variable, with differences between Sal–Boavista and S. Vicente–S. Luzia specimens.

TABLE 1

Measurements taken on *Volvarina* shells. n= number of specimens measured. L= maximum length (mm). Ws= maximum width (mm). L/Ws= shell length/shell width ratio.

| Species	Localities	n	Length (L) mm			Width (Ws) mm			Ratio L/Ws		
			Max.	Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean
V. taeniata	**Lectotype BMNH**	1			**13**			**6.1**			**2.11**
V. taeniata	Sal/Santiago/S.Antao	118	15.3	11.1	12.8	6.9	4.9	5.9	2.32	2.03	2.17
V. taeniata	Brava	3	13.8	13.1	13.6	5.7	5.5	5.6	2.51	2.29	2.41
V. taeniata	S. Vincente/S. Luzia	12	12.4	9.5	11.5	5.5	4.2	5.2	2.35	2.25	2.22
V. cessaci	Syntypes MNHN	4	11.4	10.7	10.9	5.2	4.6	4.9	2.32	2.15	2.23
V. quadripunctata	Lectotype MNHN	1			11.2			4.8			2.33
V. boyeri n.sp.	**Holotype MNHN**	1			**9.1**			**3.9**			**2.33**
V. boyeri n.sp.	Sal	9	10.5	8.8	9.4	4.8	3.7	4.1	2.38	2.19	2.29
V. verdensis	**Lectotype BMNH**	1			**9.8**			**4.6**			**2.13**
V. verdensis	Boavista/Brava/Maio	96	10.7	7.2	9.0	4.7	3.4	4.1	2.35	2.06	2.18
V. verdensis	Santiago	38	9.5	6.8	7.7	4.6	3.2	3.6	2.27	2.03	2.13
V. mediocincta	**Lectotype BMNH**	1			**6.4**			**3.0**			**2.13**
V. mediocincta	Boavista/Brava/S. Vicente	34	6.6	5.0	5.9	3.1	2.3	2.7	2.35	2.03	2.18
V. bouvieri	Syntype MNHN	1			5.5			2.7			2.04
V. corallina	**Syntype MNHN**	1			**5.0**			**2.4**			**2.08**
V. corallina	Santiago/Brava	10	6.9	5.7	6.3	3.2	2.6	2.9	2.25	2.09	2.16
V. cernita	**Syntype MNHN**	1			**5.1**			**2.4**			**2.12**
V. cernita	Boavista/Sal	105	9.5	5.9	6.9	5.0	2.9	3.5	2.14	1.90	1.99
V. cernita	S. Vicente/S. Antao	30	8.8	6.5	7.3	4.6	3.2	3.7	2.06	1.85	1.94
V. cernita	S. Luzia	6	9.8	5.8	8.4	5.0	2.7	4.3	2.14	1.87	1.96
V. nuriae n.sp.	**Holotype MNCN**	1			**10.2**			**4.5**			**2.26**
V. nuriae n.sp.	Boavista	48	10.0	8.0	8.8	4.2	3.6	3.9	2.39	2.07	2.24
V. joubini	**Syntype MOM**	1			**8.3**			**3.9**			**2.12**
V. sauliae	**Neotype BMNH**	1			**6.8**			**4.1**			**1.66**
V. sauliae	Sal	6	8.0	6.7	7.3	4.8	4.0	4.5	1.66	1.52	1.60
V. sauliae	Brava	2	8.5	8.3	8.4	4.7	4.7	4.7	1.80	1.76	1.78
V. obscura	**Lectotype BMNH**	1			**8.7**			**4.2**			**2.07**
V. obscura	Obock/Aden/Red Sea	50	11.7	8.2	9.6	5.6	3.9	4.6	2.22	1.98	2.08
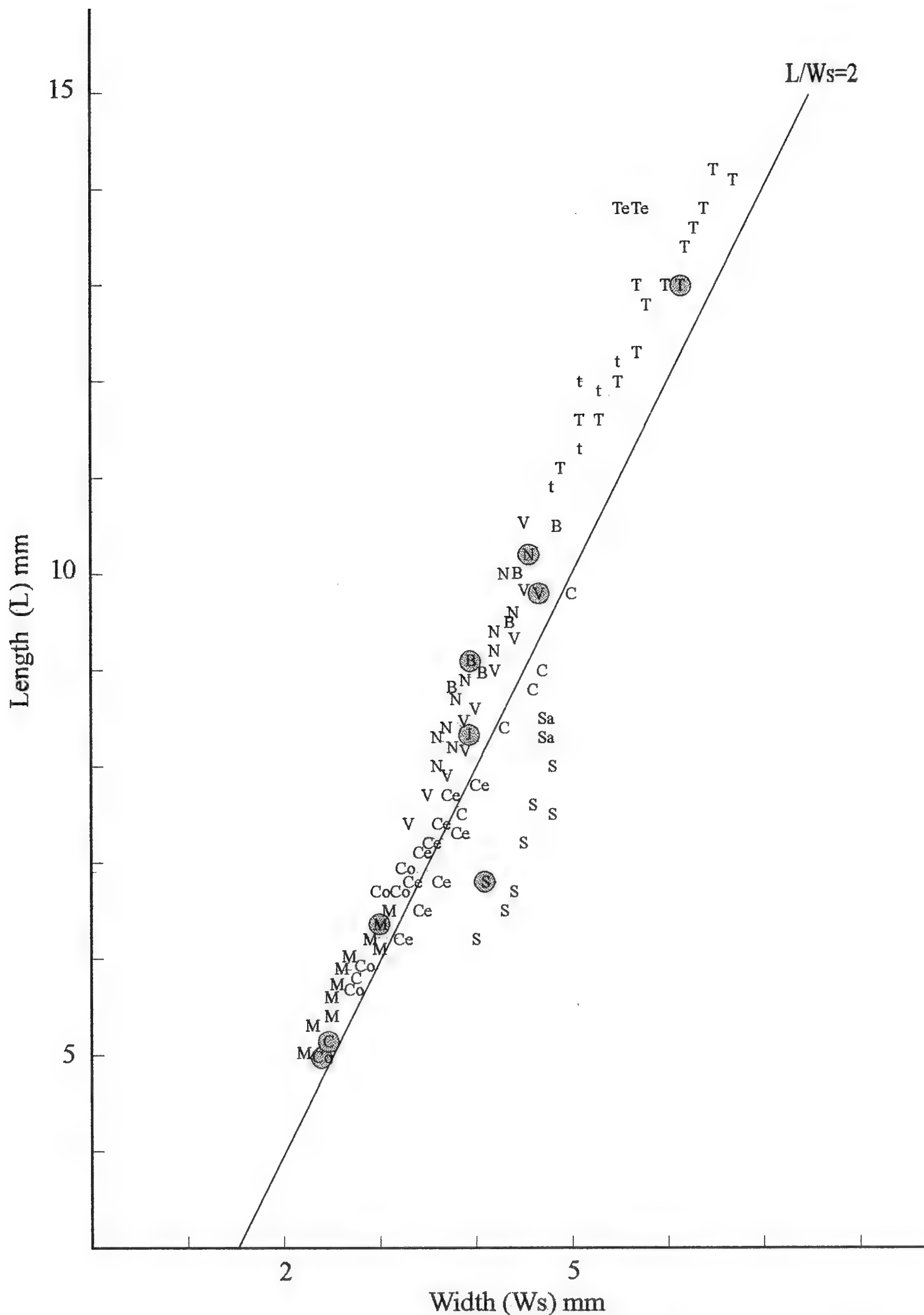
Fig. 46 Measurements taken on shells of *Volvarina* from Cape Verde Islands (type specimens with a grey circle). L/Ws ratio separates the species in clusters. **T**= *Volvarina taeniata* (Sowerby, 1846), lectotype (loc. ?) and 13 sh (Sal). **Te**= *V. taeniata* (Sowerby, 1846), 2 sh (Brava). **t**= *V. taeniata* (Sowerby, 1846), 5 sh (S. Vicente and S. Luzia). **B**= *V. boyeri* n. sp., holotype and 5 sh (Sal). **V**= *V. verdensis* (E.A. Smith, 1875), lectotype (Cape Verde Is.) and 10 sh (Boavista). **M**= *V. mediocincta* (E.A. Smith, 1875), holotype (Cape Verde Is.) and 10 sh (Sal). **Co**= *V. corallina* (Bavay, 1910), syntype (Cape Verde Is.) and 5 sh (Santiago). **C**= *V. cernita* (Locard, 1897), syntype and 6 sh (S. Vicente and S. Luzia). **Ce**= *V. cernita* (Locard, 1897), 10 sh (Sal and Boavista). **N**= *V. nuriae* n. sp., holotype and 10 sh (Boavista). **J**= *V. joubini* (Dautzenberg & Fischer, 1906), syntype (Boavista). **S**= *V. sauliae* (Sowerby, 1846), neotype (Santiago) and 7 sh (Sal). **Sa**= *V. sauliae* (Sowerby, 1846), 2 sh (Brava).

TABLE 2

Means of measurements taken on radulae of *Volvarina*. n= number of specimens studied. Wr= width of tooth (µm). H= heigth of central cusp (µm). X= height of lateral cusps (µm). Y= height of tooth base (µm). Cusps/cusps= number of cusps on each side of the central cusp. L= shell length (mm) for the specimens from which the radulae were extracted. Wr/H= tooth width/height ratio. Wr/cusps= tooth width/lateral cusps ratio. L/Wr= shell length/tooth width ratio.

Species	Locality	n	Wr	H	X	Y	Cusps\cusps	L	Wr/H	Wr/cusps	L/Wr
V. taeniata	Sal/Boavista	10	415	147	110	54	10.2\10.0	12.8	2.84	20.6	30.84
V. taeniata	S. Vincente	2	345	112	85	41	10.5\11.0	11.5	3.11	16.1	33.33
V. verdensis	Boavista/Maio	10	382	119	93	43	12.1\12.2	9.7	3.23	15.8	25.39
V. mediocincta	Sal/S. Vic./Boav.	6	182	68	51	25	8.3\8.2	6.0	2.67	11.2	3.97
V. cernita	Sal/Boavista	5	207	92	69	36	8.0\7.6	7.1	2.25	13.6	24.30
V. cernita	S. Luzia/S. Vicen.	5	346	137	102	48	5.6\5.6	8.6	2.52	31.7	24.86
V. nurtae n. sp.	Boavista	10	266	78	62	29	10.5\11.0	9.2	3.34	12.6	34.59
V. sauliae	Brava/Sal	3	148	51	43	23	9.6\10.0	8.1	2.92	7.4	54.73
V. obscura	Obock/Aden	4	355	138	97	54	7.5\7.2	9.4	2.6	24.4	26.48

Curiously, in this species larger radular teeth have fewer lateral cusps than the smaller teeth.

According to Coovert & Coovert (1990), the genus *Volvarina* has a shell length/tooth width ratio (L/Wr) between 73.24 (*V. rex*) and 25.24 (*V. rubella*). All the species studied in the present paper have a L/Wr ratio between 35.00 and 25.00, except *V. sauliae* (54.73), showing a relatively small radula, and *V. cernita*, from S. Vicente and S. Luzia (24.86), with the largest radula (proportionally) among all the *Volvarina* species known.

Feeding in *Volvarina* species from the Cape Verde islands is unknown. *V. taeniolata* Mörch, 1860, from California was observed feeding only on fresh muscle from the shrimp *Crangon dentipes*; *V. taeniolata* has radular teeth with 23 equal cusps and a "poison gland" although there is no evidence that it anesthetizes prey (Fretter, 1976).

All the studied species are endemic to the Cape Verde archipelago (9 species, except the Red Sea endemic *V. obscura*). Cosel (1982c) considered in the Cape Verde Islands 13 species of *Volvarina* (including *Gibberula jousseaumi*), 8 of them endemic. All of these taxa have been appropriately dealt with. Many of the studied species in the present paper are found on several islands (Maps. 2–7), except *V. boyeri* n. sp. (Sal endemic), *V. nuriae* n. sp. (Boavista endemic) and *V. joubini* (from SW of Boavista). We found 7 sympatric species on Boavista, 6 on Brava, 5 on Sal and Santiago, 3 on S. Vicente, and 2 each on S. Luzia, S. Antão, S. Nicolau, Fogo, and Maio (Map 8).

Species of the genus *Conus* from the Cape Verde archipelago, which present larval development with intracapsular metamorphosis as the *Volvarina* species, have a similar insular distribution (Rolán, 1991). On Boavista, there are 35 different and sympatric populations of *Conus*, 22 on Sal, 14 on Maio, 9 on S. Luzia, 8 on S. Vicente, 6 on Santiago, 1 on Brava, S. Antão and S. Nicolau, and none on Fogo.

Boavista, Sal and Maio are the oldest islands in this volcanic archipelago (Rolan, 1991), with very low relief and many beaches, and they are close to the continent. On the other hand, S. Antão, S. Nicolau, Brava and Fogo are younger, with relief comprising fully maintained volcanic structures and with recent vulcanism (the last eruption occurred on
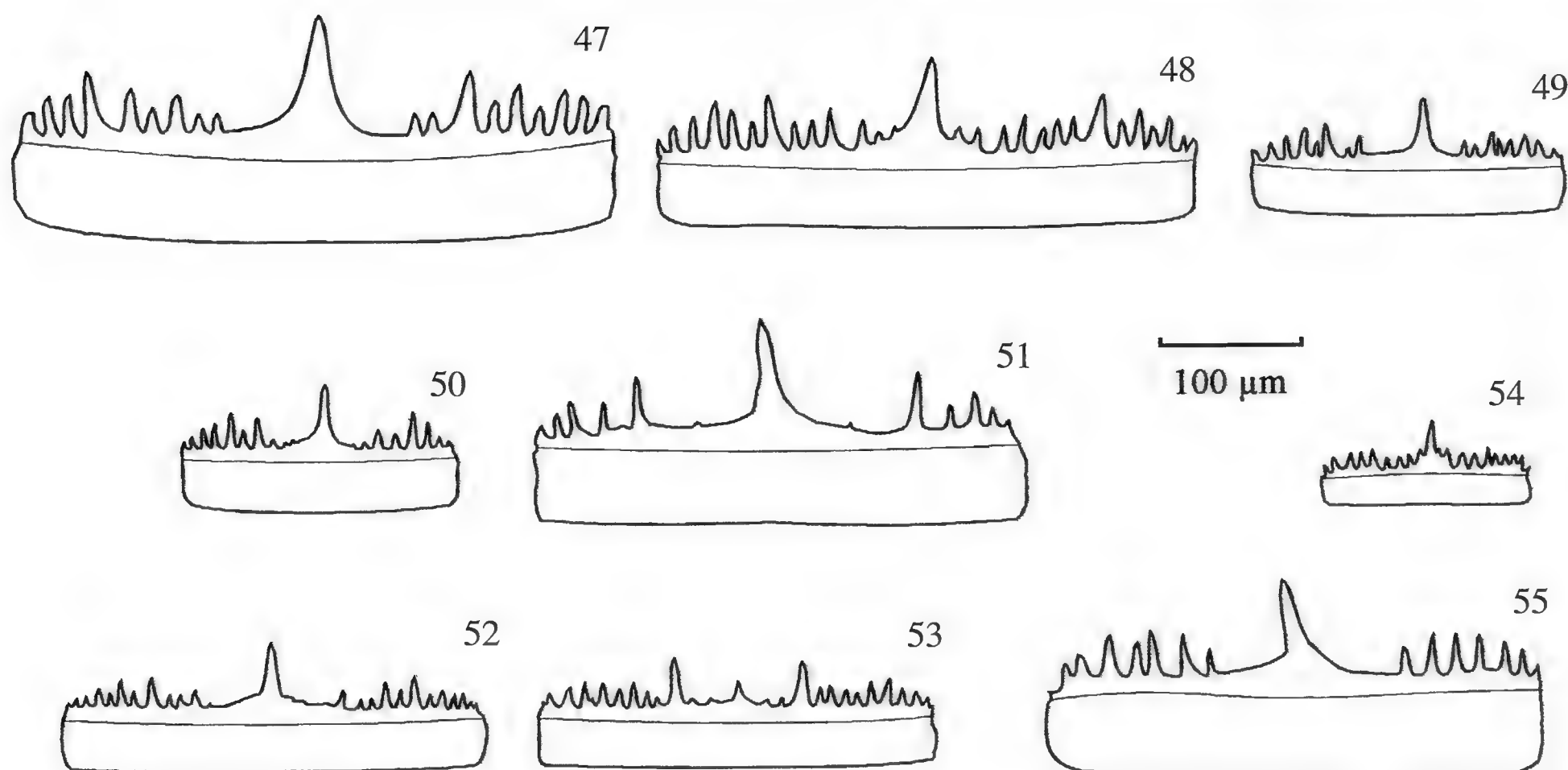
Figs 47–55 Radulae of *Volvarina*: **47** *V. taeniata* (Sowerby, 1846), Parda, Sal, tooth width (Wr)= 425 µm (shell length: L= 13.8 mm). **48** *V. verdensis* (E.A. Smith, 1875), Sal Rei, Boavista, Wr= 380 µm (L= 9.8 mm). **49** *V. mediocincta* (E.A. Smith, 1875), Gatas, Boavista, Wr= 220 µm (L= 6.1 mm). **50** *V. cernita* (Locard, 1897), Rigona, Sal, Wr= 195 µm (L= 7.1 mm). **51** *V. cernita* (Locard, 1897), Saragasa, S. Vicente, Wr= 350 µm (L= 7.8 mm). **52** *V. nuriae* n. sp., Sal Rei, Boavista, Wr= 300 µm (L= 9.6 mm, paratype 10). **53** *V. nuriae* n. sp., Sal Rei, Boavista, teratological radula, Wr= 280 µm (L= 8.9 mm, paratype 9). **54** *V. sauliae* (Sowerby, 1846), Baia Pedrinha, Brava, Wr= 150 µm (L= 8.3 mm). **55** *V. obscura* (Reeve, 1865), Obock, Djibouti, Wr= 350 µm (L= 9.1 mm).

Fogo in 1952). According to the results for *Volvarina* and *Conus*, Boavista, which is older and has more species than the other islands, may have more suitable habitats now than the other islands. In the Cape Verde archipelago the predominant currents are from NE to SW (Cosel, 1982 c; Rolan, 1991), which aids in dispersion from the oldest islands (Boavista, Sal and Maio) to the remainder.

Natural barriers, such as distance between islands, depths and currents exist (Rolán, 1991); according to this author the most important barrier (Map 8) separates S. Antão, S. Vicente, S. Luzia and S. Nicolau from the other islands. *V. boyeri* n. sp., *V. verdensis*, *V. corallina*, *V. nuriae* n. sp., and *V. sauliae* could not surmount this barrier.

However, the distribution is not totally similar to that of the genus *Conus*, with more than 40 species living in most cases in a limited area. In the genus *Volvarina* there are only two littoral species with a very limited area: *V. boyeri* n. sp. (Sal endemic, western coast), and *V. nuriae* n. sp. (Boavista endemic, Sal Rei area), while several species have a broad distribution in spite of their non– planktotrophic larval development, suggesting a limited capacity for dispersion. Thus, *V. cernita* was collected in all the islands of the Cape Verde archipelago, and possibly *V. taeniata* and *V. mediocincta* live on all the islands. The poor samples from Maio, S. Antão, S. Nicolau and Fogo were not enough to allow the species' real distribution to be known.

Distribution on S. Luzia and the eastern coast of S. Vicente had been described for several species of the genus *Conus*: *C. lugubris* Reeve, 1849; *C. decoratus* Rökel, Rolán & Monteiro, 1980; *C. saragasae* Rolán, 1986; *C. navarroi* Rolán, 1986; and *C. bellulus* Rolán, 1990 (Rolán, 1991). The barrier between S. Vicente and S. Luzia, with 42 m maximum depth, seems non–existent. In the *Volvarina* species *V. taeniata* and *V. cernita*, the shells from east of S. Vicente (Saragasa and Callhau area) and S. Luzia are almost identical. A somewhat similar phenomenon was observed in *V. verdensis* from Maio and the populations of the eastern coast of Santiago, both having a very peculiar colour shell pattern.
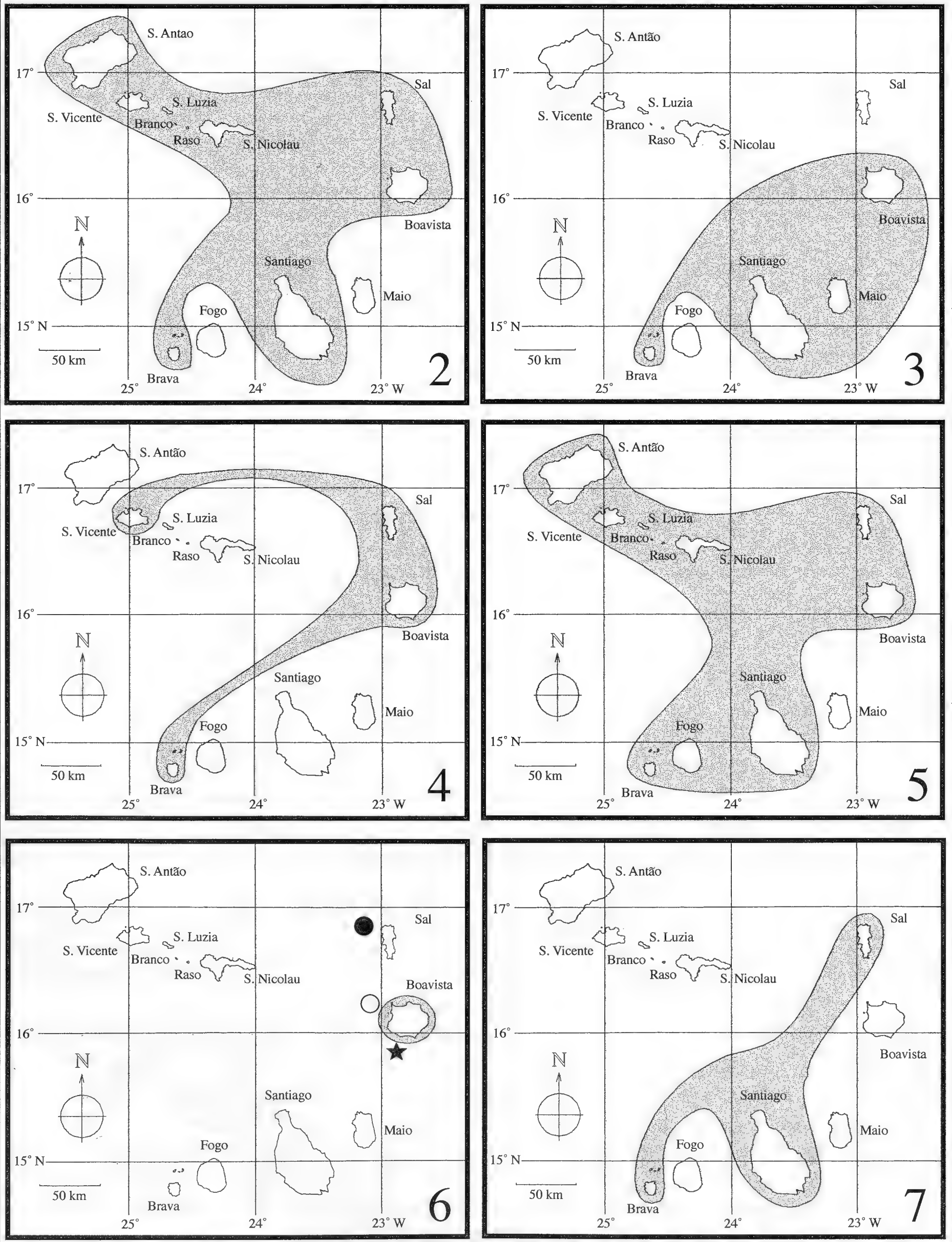
Maps 2–7 Distribution of *Volvarina* species in Cape Verde Islands: **2** *V. taeniata* (Sowerby, 1846). **3** *V. verdensis* (E.A. Smith, 1875). **4** *V. mediocincta* (E.A. Smith, 1875). **5** *V. cernita* (Locard, 1897). **6** *V. boyeri* n. sp. (black circle), *V. corallina* (Bavay, 1910) (grey area), *V. nuriae* n. sp (white circle), and *V. joubini* (Dautzenberg & Fisher, 1906) (black star). **7** *V. sauliae* (Sowerby, 1846).

Except for the very different *V. sauliae*, all *Volvarina* species from the Cape Verde Islands are closely related one to another and belong to an interesting colonization of the archipelago. An allopatric speciation could have occurred due to the numerous and neighbouring islands. The colonization of other islands subsequently took place several
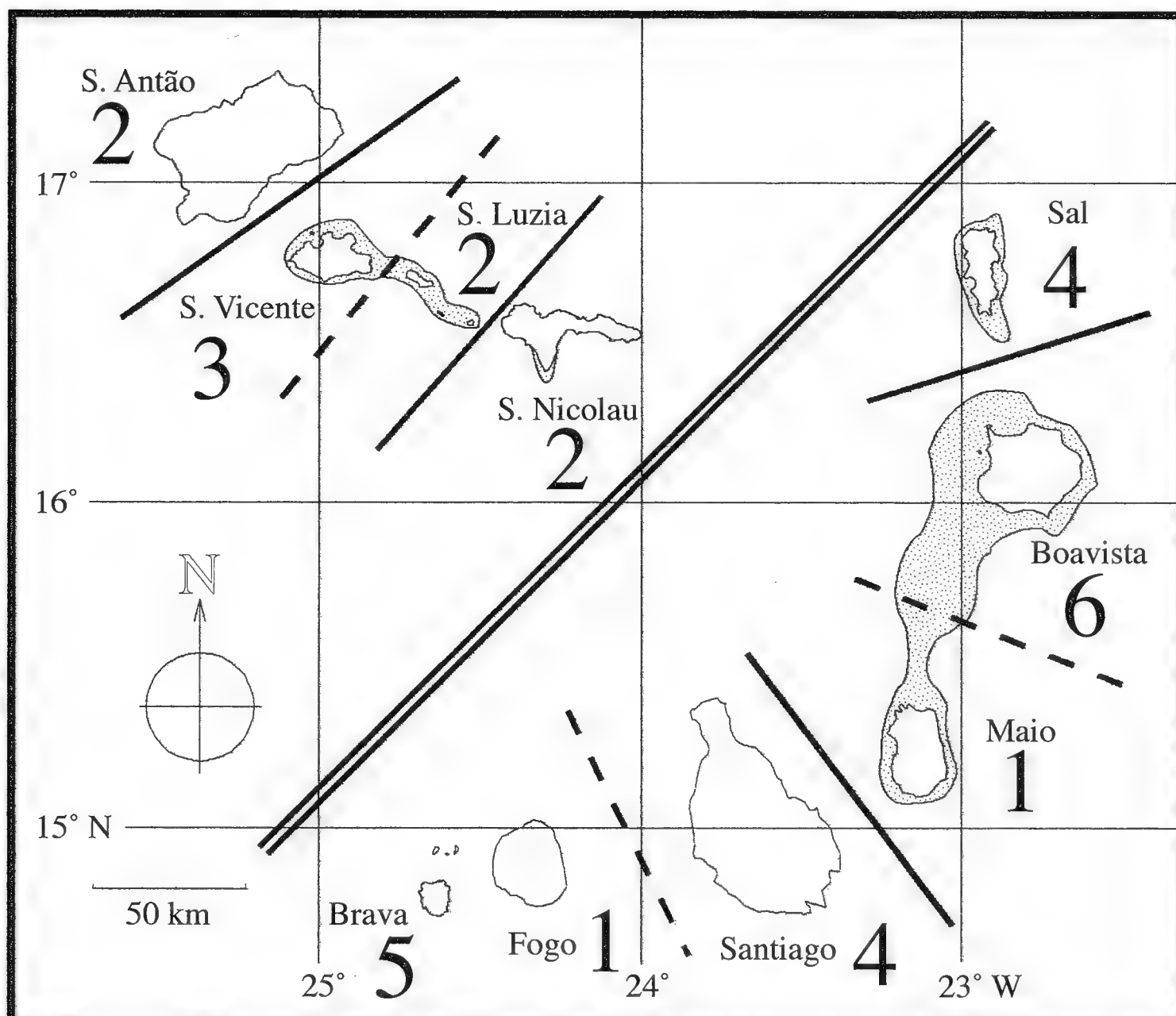
Map 8 Natural barriers between islands in Cape Verde Archipelago (Rolán, 1991). Parallel lines: very important barrier. Simple lines: important barriers. Intermittent lines: less important barriers. The numbers are the *Volvarina* species known per island and the shaded areas show the platform with depths less than 200 m.

times to reach the present distribution.

All *Volvarina* species from the Cape Verde islands have conchological characters unlike those from North–West Africa: *V. ampelusica* Monterosato, 1906, *V. attenuata* (Reeve, 1865), *V. deliciosa* (Bavay in Dautzenberg, 1913), and *V. exilis* (Gmelin, 1791); from the Mediterranean: *V. mitrella* (Risso, 1826); and from Madeira: *V. roberti* (Bavay, 1817). These species have more slender shells, with a very pale colour or no colour at all, and without pigmentation on the outer lip (Gofas, 1989: 176). The radular teeth of *V. mitrella* are also different, lacking a prominent central cusp (Gofas, 1989).

Volvarina species from the Cape Verde Islands are closely related to *V. insulana* Gofas & Fernandes, from S. Tomé and Principe, *V. peregrina* Gofas & Fernandes, 1992, from Angola, *V. oceanica* Gofas, 1989 and *V. ptychasthena* Gofas, 1989, both from Azores, and *V. obscura* (Reeve, 1865), from the Red Sea (herein). All these species usually live in shallow waters (except *V. ptychasthena*), have coloured bands on the body whorl, pigmentation on the outer lip, a relatively short spire, and radular teeth with a prominent central cusp (at least in *V. insulana*) (Gofas & Fernandes, 1992). On Azores, the *Volvarina* species live only on the oldest island of the archipelago, S. Maria–Formigas (Gofas, 1989).

In view of the fact that the shells and the radulae are very similar, *V. obscura* from the Red Sea must be closely related to the *Volvarina* species from the Cape Verde islands. Recent *Volvarina* species from mainland West Africa and the Mediterranean are not related to them. Distribution on both sides of Africa, in our case at more or less the same latitude (12° N to Djibouti and 16° N to the Cape Verde Islands), has been described in other gastropod species, such as those of the *C. venulatus* complex from the Cape Verde Islands and similar species from the Indo–Pacific Ocean (Rolán, 1991). *V. rubella* and other species from the Western Atlantic ("*V. rubella* group") have shells with a relatively

short spire and radular teeth with a strong central cusp (Coovert, 1989; Coovert & Coovert, 1990), and are also closely related to the Cape Verde Island *Volvarina* group.

Acknowledgements

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TENELLIA ADSPERSA (NORDMANN, 1845) LIVING AT ST. OSYTH IN ESSEX.

In the course of a survey of the fauna of the borrow dykes of north east Essex, a visit was made to Howlands Marsh, an Essex Wildlife Trust Reserve, near St. Osyth (51°46'N, 01°02'E) on 23rd July 1998. One of the dykes was in contact with St Osyth Creek and ultimately the sea, by means of an old sluice pipe approximately 15 cm in diameter. There was inflow and outflow of water through the sluice for about two hours either side of high tide.

A colonial hydroid was attached to the mouth of the sluice pipe on the borrow dyke side, moving in the water as it flowed in. A small sample of this hydroid was taken for identification and was found to be *Laomedea flexuosa*. A day later this specimen was examined again (with x20 stereo microscope) and a 5 mm long sea slug, very similar in colour to the *Laomedea*, was seen moving along its branches. This was subsequently identified as *Tenellia adspersa*, which is said to feed on *Laomedea*. It is worth emphasising that the *Tenellia* was not noticed in the first instance when the *Laomedea* was being identified. Other organisms living in the dyke near the sluice included *Scrobicularia plana* (numerous moving siphons were observed), *Hydrobia ulvae*, *Idotea chelipes* and *I. balthica*. *Ventrosia ventrosa* and *Ruppia maritima* became common c. 30 m above the sluice.

Two weeks later on the second visit to the site, at low tide, more *Laomedea* was noticed on the bottom of the shallow (7–8 cm deep) channel of the dyke, near the sluice. Some of this *Laomedea* was attached to stones and some was unattached and drifting along with the water flow. A piece of unattached *Laomedea* was taken and kept in a Petri dish in dim light. A few hours later, careful examination revealed another specimen of *Tenellia*, which moved down among the branches of the *Laomedea* when illuminated from above. Four tiny pycnogonids and three very small sea squirts were also present on this piece of *Laomedea*.

Tenellia adspersa has only been recorded from six localities in Britain this century[1], but our experience shows how easily it can be overlooked.

We should like to thank Ian Killeen for confirming the identity of the *Tenellia* and Jan Light for help and encouragement.

[1] *Bratton J.H.* (ed) 1991 *British Red Data Books. 3. Invertebrates other than insects.* JNCC, Peterborough.

Peter and Pam Wilson
6 St. Helena Rd
Colchester

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INSTRUCTIONS TO AUTHORS

Manuscripts should be sent to:

THE HON. EDITOR, DR P.G. OLIVER,
NATIONAL MUSEUMS & GALLERIES OF WALES, CATHAYS PARK, CARDIFF CF1 3NP.
GRAHAM.OLIVER@NMGW.AC.UK

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LAND SNAIL FAUNAS OF THE DESERTA ISLANDS, MADEIRAN ARCHIPELAGO, PAST AND PRESENT

R.A.D. CAMERON[1] & L.M. COOK[2]

Abstract   Results of three recent surveys of the land snails of the Deserta Islands, Madeiran archipelago are given, including a newly described fossil fauna on the largest island, Deserta Grande. Age estimates on shells from the sediments suggest deposition between 60,000 and 90,000 yr BP. Results are compared with 19th century records, and with similar undated fossil material from the island of Bugio, known since the 19th century. A revised annotated check-list of records is provided. The Pleistocene faunas include species now extinct on the islands, indicative of wetter and better vegetated conditions than now. The two largest islands have suffered considerable environmental degradation since their discovery, and show apparent rates of extinction over the last 150 yr much greater than in the larger islands of the archipelago, Madeira and Porto Santo. The Desertan land snail fauna is much closer to that of Madeira than that of Porto Santo, reflecting an earlier probable land connection.

Key words   Land-snails, Desertas, Madeiran archipelago, extinctions.

INTRODUCTION

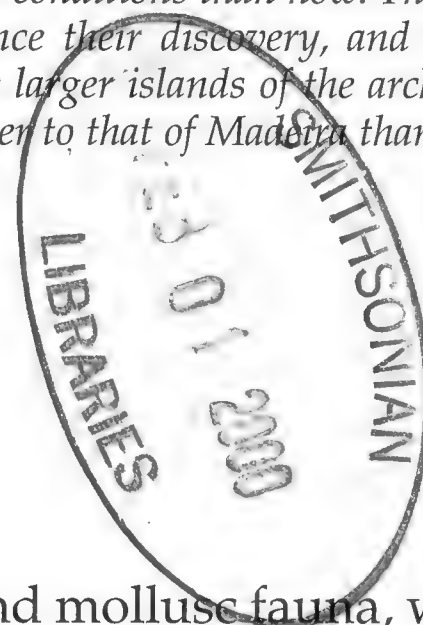The Madeiran archipelago has a rich and largely endemic land mollusc fauna, which has been the subject of detailed study for nearly two centuries (Albers, 1854; Lowe, 1854; Castello de Paiva, 1867; Mandahl-Barth, 1943; Wollaston, 1878; Waldén, 1983). In addition to a remarkably thorough account of the fauna as it was in the nineteenth century, there are substantial snail-bearing Pleistocene and Holocene deposits. Between them, these sources enable us to trace some of the natural and man-induced changes in the land snail fauna over the last 250-300,000 years. The three islands Ilhéu Chão, Deserta Grande and Bugio, known collectively as the Desertas, form a part of the Madeiran archipelago (Figure 1). Unlike the two larger islands, Madeira and Porto Santo, the islands have not been continuously inhabited since the Portuguese settlement of the early fifteenth century (Pereira, 1967; Frietas Ferraz, 1986; Goodfriend *et al.*, 1994). The topography is rugged, with few landing places and no good natural harbours. While they have been visited by malacologists, their fauna is less well known than that of Madeira and Porto Santo, and some of the nineteenth century records from them are doubtful. A rich fossil molluscan fauna from the summit of Bugio is catalogued by Wollaston (1878), but there are no dates or stratigraphy from these sediments to aid interpretation. In this paper we report on three recent visits to the Desertas, describe a dated deposit of fossil shells from Deserta Grande, and review the status of nineteenth century records. We use the information to provide an annotated check-list of the molluscan fauna of the Desertas, and to track changes in the fauna to complement the analysis of Cameron & Cook (1996) for Madeira and Porto Santo.

THE ISLANDS AND THEIR HISTORY

The islands lie on a submarine ridge extending from the Ponta de São Lourenço at the eastern end of Madeira (Figure 1 a). The location of 1997 sample sites is shown in Figure 1b. The islands probably originated in the same volcanic events as formed the peninsula, making them 0.75-4 Myr old (Mitchell-Thomé, 1985; reviewed by Cook, Cameron and Lace, 1990). This estimate is provisional, however, as the archipelago dates to 12-15 Myr in places, and we do not know of specific dates obtained for rocks on the Desertas. Ilhéu Chão is much the smallest of the three islands (*c.* 0.4 km²). Its highest point is 99

[1]Department of Animal and Plant Sciences, University of Sheffield, Sheffield S1 4ET, U.K.
[2]The Manchester Museum, Oxford Road, Manchester M13 9PL, U.K. email:lcook@fsl.scg.man.ac.uk.
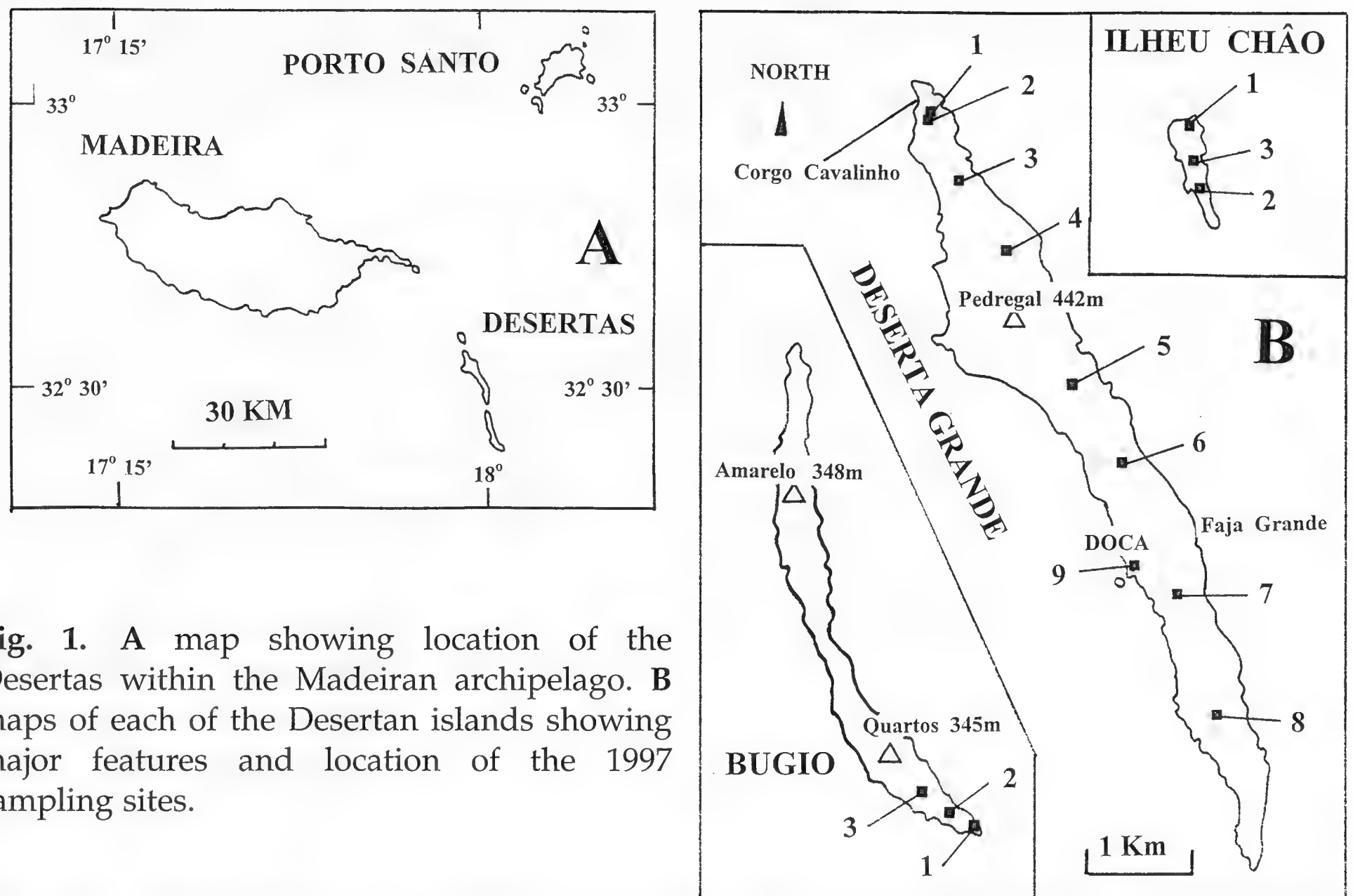
Fig. 1. A map showing location of the Desertas within the Madeiran archipelago. **B** maps of each of the Desertan islands showing major features and location of the 1997 sampling sites.

m asl., and it consists of a plateau surrounded by sea-cliffs. The plateau retains a sparse cover of grasses and low shrubby bushes. Deserta Grande is the largest island (c. 10 km²). Its highest point is Pico Pedregal (442 m asl.), situated about a third of the way down the island at its widest point (c. 1.7 km). North of, and around the summit there is a plateau, and a northwards draining valley opening over cliffs to the east before reaching the northern tip of the island. South of Pedregal, the island is narrow, with a spinal ridge (350–400 m asl.) running down its centre, which has a few small plateaux and some sharp crests. There are massive sea cliffs around most of the coast, but in the southern third of the island there are two areas of lower ground. The western one, the Doca, is a landing place and the site of the research station run by the Parque Natural da Madeira. It was formed by a massive land slip just over a hundred years ago (H. Costa Neves, personal communication). Fajâ Grande, on the east coast, appears to have had a similar origin.

Bugio (c. 3 km²) is similar in character to Deserta Grande. A single, often knife-edge ridge runs the length of the island, flanked by massive sea cliffs. The two highest peaks, Amarelo (348 m asl.) and Quartos (345 m asl.), are surrounded by tiny eroded plateaux.

Large areas of both the larger islands are devoid of vegetation, including most of the plateau around Pedregal on Deserta Grande. Smaller areas, subject to erosion around their margins, retain grasses, low shrubs and at high altitudes, some bracken *Peridium aquilinum*. There are no long-term climatic records, but the islands are arid; there are no permanent streams. They are also exceptionally windy. The aridity is tempered by frequent mists around the summits of the larger islands. The islands appear to have been treeless even at the time of their discovery. After the settlement of Madeira and Porto Santo in the early 15th century (Pereira, 1967) landings were also made on the Desertas. Cattle were kept there looked after by a few people. Ruins of farm buildings and walls can still be seen, especially on the plateau now called Cabeço da Doca. Local inhabitants repelled piratical raiders in 1503 (or perhaps 1564, Pereira, 1967). By 1590 there were eight labourers and a factor living on Deserta Grande. Permanent occupation seems to

have ceased at some later date, and in 1803 waterspouts destroyed most of the grazing land (Anon, 1945).

While there are now no cattle on the islands, there are feral rabbits, goats, rats, mice and cats. These have contributed to continuing soil erosion and suppression of plant cover. Lowe (1857) found quite a rich flora. Photographs in Pereira (1967), now perhaps 35-50 years old, show vegetation cover on Ilhéu Chão much as it is today, and perhaps marginally better than now on Deserta Grande. A recent description comparing Ilhéu Chão and Deserta Grande has been made by Hampshire (1984). The vegetation of Deserta Grande and of the Madeiran peninsula is similar and both differ somewhat from Ilhéu Chão. This is partly because *Mesembryanthemum crystallinum* L. and *Suaeda vera* Forssk. were both once cultivated on the smaller island for burning to yield soda (Lowe 1857; Hampshire 1984). Also, rabbits have long been absent from Ilhéu Chão while they are abundant on the peninsula and have been until very recently on Deserta Grande. Pereira catalogues a number of unsuccessful attempts at afforestation of these islands, of which the only relic is a solitary agarve just north of Pedregal (Figure 1b). During this century, temporary residents have included fishermen, hunters, watchers for the whaling industry and military personnel, always in very small numbers.

The authorities of the Parque Natural da Madeira, which includes all of the Desertas, have recently undertaken a programme to eradicate introduced mammals. Rabbits have been eliminated from Deserta Grande, goats are being hunted to extinction and some recovery of vegetation has been observed (B. Bell and H. Costa Neves, personal communications).

MATERIAL, SAMPLING AND NOMENCLATURE

Wollaston (1878) has been used as an authoritative source of nineteenth century records, and for the fossil fauna on Bugio. We argue below that some records he himself doubted should be deleted for analytical purposes.

For twentieth century records we have used our own survey data, supplemented by published information from Hemmen and Groh (1986) and Neubert and Groh (1998), which is derived from a visit made in 1985. They refer to fossil material from Deserta Grande, but give no details of the deposits or their location. Our own records come from three visits, (a) that reported in Cook, Jack and Pettitt (1972), based on collections made in summer 1970, (b) by Cook and L.A. Lace in summer 1981, the material being discussed in Cook *et al.* (1990).

In 1970 and 1981 sites were searched for between ½ and 1 hr by two people, but material was not collected for sieving. The results of these two surveys have been pooled to represent (i) the whole of Ilhéu Chão, (ii) Deserta Grande from its northern tip to Pedregal, (iii) Deserta Grande from the Doca to its southern tip and (iv) Bugio from its southern extremity to the southern slopes of the Quartos peak.

(c) By the authors together in July 1997, when sample sites *c.* 30 m x 30 m were searched for about 1 hr, and soil and litter removed for sieving. These sites are shown in Figure 1b.

All sampling sites were made in rocky, open habitats with sparse vegetation, which is all that is available. Vegetation cover was better on Ilhéu Chão and the northern part of Deserta Grande than elsewhere. The fossil samples (labelled Deserta Grande 2a-d) come from an exposed fossil soil at the summit of the scree slope leading to the plateau from the Corgo Cavalinho. This eroding exposure extended in a nearly horizontal arc round a truncated valley descending to gullies in the northern cliffs of the island. Most of it was partially obscured by debris, but a section *c.* 3 m long was exposed to a depth of 1 m (Figure 2). It was well-stratified, with calcreted root-systems in place. The material was hard, and shells were excavated from it individually. Samples 2a and 2b came from this short exposure; 2c represents pickings from a further 50 m of partial exposure, and
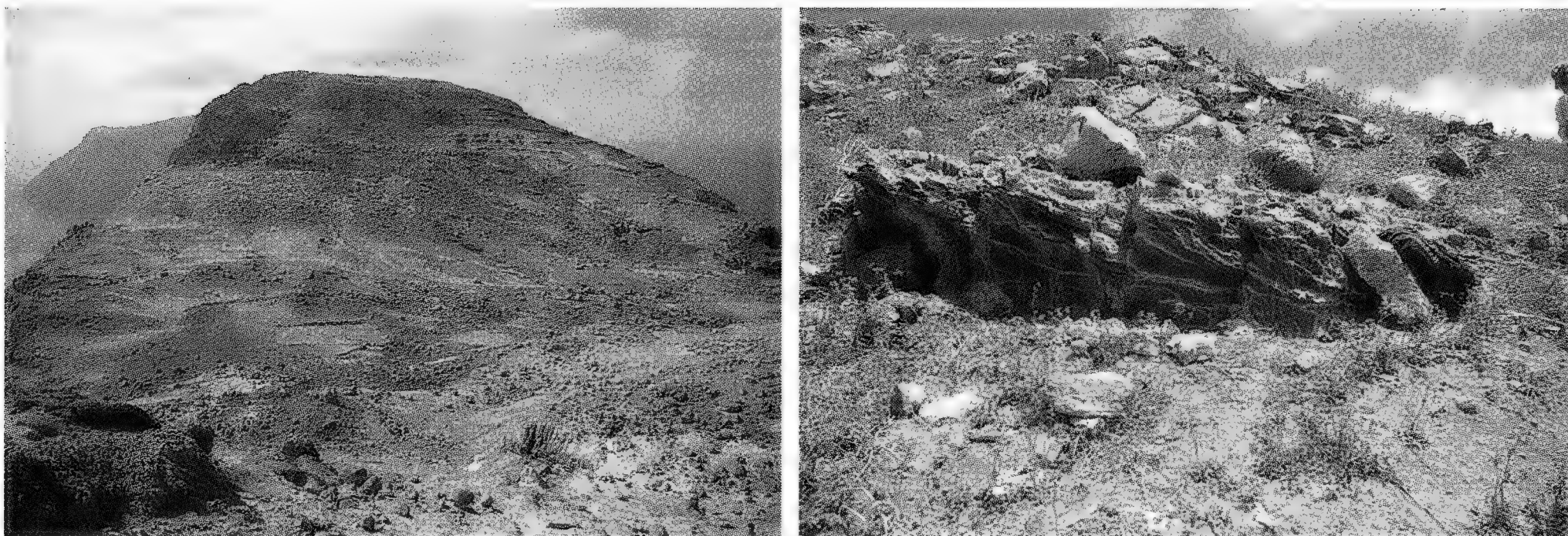
Fig. 2. Structure and habitat on Deserta Grande. **Left** Plateau on southern part of the island above the Doca, showing evidence of past human activity. To right, a circular area known as a threshing floor, possibly a dew pond, centre left, walled enclosures, probably for animals. **Right** Fossiliferous deposit at north end near site 1. Figure at extreme right gives scale. The vegetation is typical of the northern plateau in summer.

2d loose shells at the base which appeared to have been washed out.

Eight shells of *Actinella nitidiuscula* from these samples were given to Dr G.A. Goodfriend for amino acid racemization determinations, in order to compare them with age-calibrated ratios from the same species in Pleistocene deposits on Madeira (Cook, Goodfriend and Cameron, 1993). Methods for determination were as described in Goodfriend *et al.* (1996).

Wollaston (1878) refers to ancient shells as subfossil. This is presumably to distinguish them from shells in which the original composition has been entirely replaced by the matrix of the deposit. That has not happened with the material examined, indeed age estimation from the racemization ratio is only possible because some protein remains, and the shells are usually easily separable from their sandy surroundings even when the surrounding is compacted. No clear distinction can be made, however, between levels of replacement by matrix, and here we have always used the term fossil for shells preserved in wind-borne or sedimentary deposits. For nomenclature we have in general followed Waldén (1983), with later additions, but with the following changes. Waldén (1983) downgraded three species described by Lowe to subspecies, despite their acceptance by Wollaston (1878). Thus, *Leiostyla macilenta* became *L. recta macilenta* and *Leptaxis vulcania* and *L. leonina* became *Leptaxis undata vulcania* and *L. undata leonina* respectively. He advanced no evidence for these changes; the taxa are clearly distinguished in Wollaston (1878), and we have retained their original status. These and other taxa (e.g. *Amphorella* species) are ripe for revision using modern methods.

Bearing in mind Lace (1992) and Cook and Lace (1993), we have not used the generic name *Steenbergia* Mandahl-Barth 1943, and include taxa assigned to it in *Heterostoma*. There is a genital dimorphism within and between *Heterostoma* populations, with some evidence of reproductive isolation between euphallics and hemiphallics (P. Craze, in preparation). Desertan populations have not been studied in this respect, and are regarded here as part of a probable *H. paupercula* complex. Finally, we have made use of the name *Paralaoma caputspinulae* (Reeve, 1852) in place of *Punctum pusillum* (Lowe, 1831) following Roth (1987). Nomenclatural authorities for all species mentioned are given in the appendix, which is an annotated check-list.

TABLE 1

Land snails found live on the Desertas. C, samples made by Cook, 1970/81 on Chão and Bugio. N, north end, S, south end and for similar samples on Deserta Grande. Numbers, 1997 samples. T, 1970-97 occurences by island. W, occurrences by island recorded in Wollaston (1878). P, records on Paiva's authority only (see text). ?, see appendix. Names in italics: no late 20th Century records. Groh and Hemmen (1986) - G in the table - state that G. coronula and G. grabhami are recent, but do not give details.

	CHÃO						DESERTA GRANDE												BUGIO					
	C	1	2	3	T	W	N	1	3	4	5	6	9	S	7	8	T	W	C	1	2	3	T	W
Leiostyla macilenta								X	X		X		X				•	O		X	X	X	•	O
Leiostyla millegrana								X	X	X		X	X				•	O						
Lauria cylindracea												X					•	O					•	O
Paralaoma caputspinulae													X				•	O						O/P
Discus guerinianus																		O/P						O/P
Vitrea contracta										X							•	O						O/P
Janulus bifrons			X			X		X	X	X	X							O						O
Cecilioides acicula																			X				X	O
Amphorella tornatellina											X	X	X				•	O/P						O/P
Amphorella mitriformis				X	•	O		X	X	X	X	X	X				•	O	X	X	X	X	•	O
Amphorella producta																	•	O					•	O
Amphorella gracilis					•	O		X	X								O	O		X	X	X		O/P
Geomitra grabhami																	G?	O					G?	
Geomitra coronula																								
Heterostoma paupercula	X	X	X	X	•	O		X	X	X	X	X	X	X	X	X	•	?	X	X	X	X	•	O
Boettgeria jensi								X	X	X			X		X		?	?	X				O	O
Boettgeria deltostoma	X	X	X	X	•	O		X	X	X	X	X	X	X	X		•	O		X	X	X	•	O/P
Caseolus abjectus																		O/P		X	X	X	•	O
Caseolus micromphalus	X			X	•	O		X	X	X	X	X	X	X	X		•	O					•	O
Caseolus punctulatus																	•	O	X				•	O
Actinella actinophora		X	X	X	•	O		X									•	O	X				•	O/P
Actinella laciniosa	X	X	X	X	•	O		X	X	X			X				•	O						O
Actinella nitidiuscula	X	X	X	X	•	O		X	X	X	X		X		X		•	O	X	X	X	X	•	O
Discula polymorpha	X	X	X	X	•	O		X	X	X	X	X	X				•	O		X	X	X	•	O
Discula tetrica																								O/P
Discula lyelliana																		O						O/P
Leptaxis erubescens	X	X	X	X	•	O		X	X	X	X	X	X	X			•	O		X	X	X	•	O
Leptaxis vulcania	X	X	X	X	•	O		X	X	X	X	X	X	X	X	X	•	O		X	X	X	•	O
Leptaxis leonina															?	?	?							
TOTAL	8	8	7	8	9	9	9	11	10	8	4	6	13	4	5	2	17	23	8	8	8	8	12	20
TOTAL (T+W)						9												25						22

RESULTS

THE STATUS OF THE NINETEENTH CENTURY RECORDS

Wollaston (1878) gives lists of living land snail species found on each island, and a fossil catalogue for Bugio. In his text he expresses considerable doubts about a number of records for which Paiva (Barão Castello de Paiva) is the only authority. He excludes three species found live, and one fossil from his lists, while mentioning them in the text. It is hard to see what criteria were applied for exclusion, since doubts expressed about some records left in seem equally strong. All these records, with appropriate notes, are included in the appendix.

Wollaston's doubts concern locality rather than identification. Paiva used paid collectors, and Wollaston doubted their reliability; he provides convincing evidence that confusion did occur in specific instances. Many of these "Paiva only" records are biogeographically or ecologically surprising, and they have the effect of crediting Bugio (3 km²) with 31 species, while Deserta Grande (10 km²) has only 22. Bugio has no obvious peculiarity with which to account for such greater diversity. While it would be possible to discount all such records, evidence from our own sampling on Deserta Grande indicates that such a course would be unjustified. Three species recorded on that island in the nineteenth century rest on Paiva's authority alone; two have been found live by us, and the third in fossil condition (Discus guerinianus). We have therefore excluded, from Bugio only, records resting on Paiva's authority which do not occur on Deserta Grande. We have made an exception for the live record of Discula tetrica, endemic to Bugio, which Wollaston found fossil. He appears to have seen Paiva's specimens and was happy about their status. All records thus accepted are included in Table 1. Those resting only on Paiva's authority are marked as such.

LATE TWENTIETH CENTURY FAUNA

Table 1 shows the species found at each site investigated in 1997 together with data from the earlier surveys as indicated above, with data from Hemmen and Groh (1986) and Neubert and Groh (1998), and with all nineteenth century records accepted by us.

The fauna of Ilhéu Chão appears to be unchanged from that recorded in the previous century. For the other two islands we have added one species to each island (but none to the Desertas as a whole), but have failed to find a number of species known in the last century. Only a small part of Bugio was searched, but the rest of the island, as seen from offshore, did not appear to differ in the limited range of habitats available. On Deserta Grande, site 9, at the Doca, is the richest, and sites north of Pedregal are richer than those in the south, where summit plateaux are now mainly bare rock.

FOSSIL FAUNA

(a) Composition - Table 2 lists the species found in the exposed horizons on Deserta Grande, the finds on Bugio reported in Wollaston (1878), and indications of their present status. Three species, Craspedopoma mucronatum, Spirorbula squalida and Actinella arcinella, have never been recorded live on the Desertas, and the record of Actinella actinophora living on Deserta Grande is based on a single specimen found by Wollaston. Discus guerinianus and Geomitra grabhami are recorded alive in the nineteenth century, but were not found by us.

Paiva (1867) records Discula lyelliana as fossil on Deserta Grande. His record is rejected by Wollaston (1878) as a long dead but recent example, because Wollaston knew of no deposits on the island. Paiva's locality, Castanheira, is however, close to the site of the deposits we found. Hemmen and Groh (1986) also record G. tiarella as fossil on Deserta Grande, but give no further locality.

The nineteenth century list from Bugio contains nine of the species found on Deserta Grande. It excludes Caseolus calculus, recorded by Paiva but rejected by Wollaston.

TABLE 2

Fossil species found on Deserta Grande and Bugio. 2b: bottom 70cm of stratum exposed; 2a: top 30 cm in small section 1m high and 3m long. 2c: 50m of stratum corresponding to 2a. 2d: loose material, apparently fossil. *G. tiarella* recorded by Hemmen and Groh (1986), *D. lyelliana* by Paiva (see text). L: found live in 20th C. by RADC/LMC. LG: found live in 20th C. by Groh. LP: found live in 19th C. by Paiva. LW: found live in 19th C. by Wollaston. The Bugio records are extracted from Wollaston (1878).

Species	Deserta Grande						Bugio	
	2b	2a	2c	2d	T	status	T	status
Craspedopoma mucronatum	+	+			+		+	
Discus guerinianus	+		+		+	LP	+	
Janulus bifrons	+	+	+		+	L	+	L
Amphorella mitriformis							+	LW
Boettgeria cf. *deltostoma*							+	L
Heterostoma paupercula			+	+	+	L	+	L
Geomitra tiarella					(+)			
Geomitra grabhami	+	+	+	+	+	LG		
Geomitra coronula							+	LG
Spirorbula squalida			+		+			
Caseolus micromphalus	+		+	+	+	L	+	L
Caseolus punctulatus							+	L
Actinella actinophora		+	+		+	LW	+	LP
Actinella arcinella		+	+	+	+			
Actinella nitidiuscula	+	+	+	+	+	L	+	L
Discus polymorpha			+	+	+	L	+	L
Discula lyelliana					(+)	LW		
Discula tetrica							+	LP
Leptaxia erubescens		+	+		+	L	+	LP
Leptaxis vulcania		+	+	+	+	L		
Leptaxia leonina							+	L
Total	**6**	**8**	**12**	**7**	**15**		**15**	

(b) *Dating* - Table 3 shows the amino acid racemization ratios of the eight *Actinella nitidiuscula* shells sent to Dr Goodfriend. One shell (CF-186) from 2d gave an anomalous result. It is clearly recent and has been excluded from further analysis. Dr Goodfriend noted it as larger and modern-looking, fossil *A. nitidiuscula* from Bugio are referred to as *A. n. saxipotens* by Wollaston (1878), a form characterized by its small size. The description fits the other seven specimens. 2d consisted of loose shells collected from the base of the deposits.

TABLE 3

Amino acid (A/I) racemization ratios for *Actinella nitidiuscula* shells from fossil deposits on Deserta Grande, with comparitive data from Madeira (Goodfriend *et al.*, 1996). Sample 19.1 is a radiocarbon date; 11.2 and 15.4 are Uranium/Thorium dates. CF-186 is a probable recent inclusion (see text).

Desertan calibrations			Madeiran calibrations		
Reference no.	Site	A/I ratio	Site	A/I ratio	Date (yr B.P.)
CF-180	2a	0.397	19.1	0.297	>47000
CF-181	2a	0.351	11.2	0.399	65000±11000
CF-182	2b	0.391	15.4	0.410	95000±12000
CF-183	2b	0.324			
CF-184	2c	0.307	**Coefficients of variation (%)**		
CF-185	2c	0.426	**Site**	**C.V.**	**n**
CF-186	2d	0.009*	19.1	12.1	5
CF-187	2d	0.428	11.2	12.5	3
Mean, excluding CF-186		0.375	15.4	3.9	6
C.V. (%)		12.9			

The coefficient of variation recorded for the remaining seven ratios is large enough to suggest a span of time over which the shells accumulated, but not so large as to suggest gross reworking of sediments. Results are comparable to Madeiran samples with similar A/I ratios. Comparison with Madeiran samples, where other forms of dating are available for comparison, suggest an age between 60,000 and 90,000 years B.P. On this small sample, there is no evidence that the upper and lower parts of the exposed horizon differ much in age.

DISCUSSION

(a) *Sampling efficiency* - There are some clear differences in species records between our survey and those of the nineteenth century. In particular, we have failed to confirm a number of earlier records from Bugio and Deserta Grande, even after discounting doubtful records from the former. Before discussing differences in terms of extinctions, it is necessary to consider our efficiency.

Two pieces of evidence suggest that our sampling techniques are adequate. On Ilhéu Chão, where degradation is least marked, our records match those of the previous century exactly. A similar intensity of sampling on Porto Santo (*c.* 1.5 samples km^{-2} compared with *c.* 1 sample km^2 here) by the same workers recorded nearly all the known nineteenth century records for that island (Cameron and Cook, 1996).

Conversely, the extensive habitat degradation on Bugio and Deserta Grande might result in extreme fragmentation of ranges rather than outright extinction, increasing the risk of missing a surviving species. Some species are hard to find: *Cecilioides acicula* is subterranean, as are resting *Geomitra* species. We sampled in summer, when many species aestivate.

The discrepancy between the nineteenth century and our records is greatest on Bugio. Seven of the 20 nineteenth century records from that island accepted by us rest on Paiva's authority; none of these 7 were found by us. But of 11 species recorded by us overall, 3 were not found in 1997, and 3 others only in 1997, even though the same part of the island was involved. These limitations need to be remembered in the following sections.

(b) *Changes in the fauna since the late Pleistocene* - There are close similarities between the fauna of the dated deposit on Deserta Grande, and that of the undated deposits on Bugio. It seems reasonable to assume that the latter are approximately the same age as the former. In the fossil sequences on Madeira (Cook *et al.*, 1993; Goodfriend *et al.*, 1996) assemblages of this age reflect a wetter and/or taller vegetation environment than that seen today. On Madeira, *C. mucronatum, A. actinophora* and *D. guerinianus* are associated with forest, or at least humid environments. *C. mucronatum* is only known as a fossil from Porto Santo, which has lost its natural tree cover (Cameron, Cook and Hallows, 1996; Seddon, 1995). Most species of *Geomitra* are found more frequently and abundantly as fossils than recent in both Madeira and Porto Santo (Cameron *et al.*, 1996; Cook *et al.*, 1993). *Spirorbula squalida* occurs in both damp and arid environments on Madeira (Cameron and Cook, 1998). The overall pattern, even compared to the nineteenth century, is of a more humid environment with better vegetation cover, but one open enough to support characteristic open-country species such as *Discula polymorpha* and *Heterostoma paupercula* (Cook *et al.*, 1993). Endemic species found live but not fossil are, with the exception of *Caseolus abjectus,* mostly small or thin-shelled.

TABLE 4

Extinctions in Desertan land snails based on (a) survival of species known fossil, (b) survival since Wollaston's (1878) monograph. Comparative data for Porto Santo and Madeira modified from Cameron and Cook (1996), The Madeiran and Porto Santan figures involve endemics only. No non-endemics appear to have become extinct; adding them would increase disparity in extintion rates.

A. Extinctions of species known fossil.

	Deserta Grande	Bugio	Combined	Porto Santo	Madeira
fossil	15	15	21	54	42
not found alive	4(27%)	2(15%)	4(19%)	14(26%)	11(26%)
not found 20th C.	3(20%)	4(27%)	5(24%)	1(2%)	3(7%)
surviving	8(53%)	9(60%)	12(57%)	39(72%)	28(67%)

B. Extinctions of species known alive in the 19th C.

	I. Chão	Deserta Grande	Bugio	Combined	Porto Santo	Madeira
alive, 19th C.	9	24	21	29	54	80
unseen 20th C.	0	7	10	8	1	9
surviving	9	17	11	21	53	71

(c) *Changes in historic times* - Table 4 shows the apparent extinction rates for Pleistocene to 19th century, and from the latter to the present, based on all 19th century records accepted by us. It also gives comparative data for Madeira and Porto Santo, modified from data in Cameron and Cook (1996). Allowing for the small volume of Desertan material, rates of apparent extinction between the Pleistocene and the 19th century are rather similar in all cases, but the change in the last 100-150 yr is clearly greater on the Desertas (collectively) than on Madeira or Porto Santo.

Within the Desertas, Ilhéu Chão appears to have suffered no loss; it retains reasonable vegetation cover. Deserta Grande and Bugio have suffered considerable losses; those on the latter may be exaggerated by factors considered above. Both islands have experienced continuous environmental degradation until very recently. The contrast with Porto Santo is striking. Porto Santo has lost its natural tree cover, has suffered considerable soil erosion, and has populations of introduced grazing and snail-eating mammals. It is, however, larger (*c.* 40 km² compared with Deserta Grande 10 km²), and it has gentler slopes, more surviving maquis-type vegetation and more varied topography providing more refuges. Soil erosion and human disturbance have produced disjunct distributions where fossil data indicate more continuous ranges in the past (Cameron *et al.*, 1996). Small islands have fewer refuges than large ones.

Only four species found on the Desertas, accepted by us, are species with wide distribution beyond the archipelago. While some species with wide distributions reached the archipelago before man (Cook *et al.*, 1993), most such species are introduced, and their numbers are dependent on the extent of human settlement and commerce. Ilhéu Chão has no species with such wide distributions.

Not all environmental disturbance is hostile to snails. The area around the Doca, created by a landslip, contains nearly all the snail species found on the whole of Deserta Grande during our 1997 visit, and is the richest single site. Gentle slopes, appreciable vegetation cover and boulders and rocks under which snails can shelter are concentrated at this site. With the success, so far, of the programme of mammal extermination carried out by the Parque Natural authorities, vegetation is recovering in places. Species at present thought to be extinct may reappear from small and undetected refuges.

(d) *Biogeography* - The native snail fauna of the Desertas, taken as a whole, shows much stronger affinities to that of Madeira than of Porto Santo (Table 5). Not only is it likely that the submarine ridge connecting the islands to Madeira was exposed at Pleistocene sea-level lows, but it is also likely that a more substantial connection has been broken by landslips and erosion (Neubert and Groh, 1998). Porto Santo, by contrast, is separated from the rest of the archipelago by a deep submarine trench. Of the present Desertan fauna only *Caseolus punctulatus* and *C. abjectus* are found alive on Porto Santo and not on Madeira, although both occur as fossils on Madeira. The absence of *C. punctulatus* from Deserta Grande and Ilhéu Chão is enigmatic; it occurs both live and fossil on Bugio.

TABLE 5

Affinities of Desertan snails (fossil and recent) other than those found outside the archipelago. Of the four widespread species excluded, all are also found on Madeira and two on Porto Santo.

	Found elsewhere	Endemic to Desertas (closest relatives)	Total
Madeira only	12	3	15
Maderia & Porto Santo or unknown	6	6	12
Porto Santo only	1	1	2
total	**19**	**10**	**29**

There is limited geographical differentiation between the Desertan islands themselves, and the status of some forms (species, subspecies or local variants) is hard to determine on the material available. Each of the two larger islands has a large, single island endemic *Discula*, and each has its own species of *Geomitra*. *Amphorella mitriformis* on Deserta Grande appears to be replaced by *A. producta* on Bugio, but, subject to taxonomic review, both these species occur elsewhere in the archipelago. *Actinella laciniosa* appears to be confined to Ilhéu Chão, but there is a nineteenth century record for the extreme north of Deserta Grande. *Leptaxis erubescens* and *Discula polymorpha* both show considerable local variation between and within islands (Wollaston, 1878; Cook *et al.*, 1990), and some of these forms are credited with subspecific rank (Waldén, 1983). The status of *L. vulcania* and *L. leonina* is also unclear. The former occupied Ilhéu Chão and the northern part of Deserta Grande, the latter the south of Deserta Grande and Bugio. Wollaston (1878) hints at clinal variation or anomalous populations on Deserta Grande. Our material is inadequate to tackle this problem. There is a parallel in the distribution of *Boettgeria* species, with *B. deltostoma* occurring on Ilhéu Chão and Deserta Grande, while the latter and Bugio hold the newly described *B. jensi* (Neubert and Groh, 1998).

Past attempts at settlement and cultivation would have involved the movement of building materials, plants and fodder from one place to another. Cook *et al.* (1990) noted the variation in shell size and sculpture in *Discula polymorpha* from different parts of the Ponta de São Lourenço and the Desertas. Compared with Madeira, the Desertan shells tend to be larger, flatter and more keeled. Shells from Ilhéu Chão were smaller than those from Deserta Grande, but similar to them in apical angle and surface sculpture. At the southern end of Deserta Grande, however, some samples differed from those at the northern end and resembled some from the Madeiran peninsula. This may be further evidence of the divergence between the two parts of the island, but the species is one which could easily be transported in the course of agricultural activity. *Heterostoma paupercula* and the *Cochlicella* species (*C. acuta* or *C. barbara*), recorded for Bugio by Paiva and doubted by Wollaston, are two others which could readily be moved by man. The revision of the species lists presented here results in a more conventional species/area relationship than that derived from Wollaston's catalogue. The latter was used by Cook *et al.* (1972) to calculate a species/area curve for the whole archipelago. Using corrected

figures makes little difference to the general character of the relationship (but improves the correlation and statistical significance). This relationship will be analysed in detail elsewhere (Cameron *et al., in preparation*).

ACKNOWLEDGEMENTS

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APPENDIX - ANNOTATED CHECKLIST OF DESERTAN LAND SNAILS

CONVENTIONS

Square brackets: records from Paiva only, rejected in this paper (see text p. 6)

Non-endemic: not confined to the Madeiran archipelago. *Heterostoma paupercula* is regarded as endemic, although it occurs elsewhere in Macaronesia.

19c: Records given in Wollaston (1878) not subsequently confirmed.

20c: Latest records made 1970-1997.

F: Fossil (records for Deserta Grande (1997) and Bugio (19th Century) only)

M: also found on Madeira; **P:** also found on Porto Santo

C: Chão; **DG:** Deserta Grande **B:** Bugio

*: only known fossil from the Desertas

Only two records from 1997 are additions to Wollaston's (1878) catalogue: *Vitrea contracta* on DG and *Leiostyla macilenta* on B. Waldén refers to Waldén (1983) and Wollaston to Wollaston (1878).

Family classification follows Waldén (1983). The Helicidae, as used by him, is split by some into a number of families, all within the Helicoidea.

SPECIES LIST

FAMILY CYCLOPHORIDAE

* *Craspedopoma mucronatum* (Menke 1830) M. P (F only). F only D.G. & B

FAMILY PUPILLIDAE

Leiostyla macilenta (Lowe 1852) DG and B, both 20c. Waldén treats as a subspecies of *L. recta* (Lowe 1852) which is M. (see text, p. 4). Desertan endemic. Not found on B in 19c. Absence from C is noteworthy.

Leiostyla millegrana (Lowe 1852) M. DG 20c, B 19c

Lauria cylindracea (Da Costa 1778) Non-endemic. DG 19c. B 19c Paiva only, accepted.

[FAMILY VALLONIIDAE]

[*Vallonia pulchella* (Müller 1774)] Non-endemic, B 19c, Paiva only, rejected.

FAMILY ENDODONTIDAE

Paralaoma caputspinulae (Reeve, 1852) Widely known synonyms are *Punctum pusillum* or *Toltecia pusilla* (both (Lowe, 1852)); see Roth (1987). Non endemic. DG 20c

Discus guerinianus (Lowe 1852). M. F DG and B. DG 19c on Paiva's authority, accepted, with the possibility that F material was collected loose from the surface. Specimens from the Desertas are referred to the subspecies *D. g. calathoides* (Lowe 1863) (Waldén).

FAMILY ZONITIDAE

Vitrea contracta (Westerlund 1871). Non-endemic. DG 20c; B 19c on Paiva's authority, accepted.

Janulus bifrons (Lowe 1831). M. F DG & B; 20c DG & B.

FAMILY FERRUSSACIIDAE

Cecilioides acicula (Müller 1774). Non-endemic. DG 19c; B 19c on Paiva's authority, accepted. Absence from 20c records likely to be accidental.

[*Amphorella melampoides* (Lowe 1831)]. B. 19c on Paiva's authority, rejected. *A. melampoides* is a rare P endemic. Wollaston excludes it from his Desertan catalogue.

Amphorella tornatellina (Lowe 1831) M, P (doubtful) DG 20c, B 19c on Paiva's authority. Paiva is also the only 19c authority for DG. *Amphorella* is in need of revision/ redescription.

Amphorella mitriformis (Lowe 1852) M, P (doubtful), C 20c, DG 20c, B 19c and F. DG specimens are typical.

Amphorella producta (Lowe 1852). M. B 20c. Appears to replace *A. mitriformis* on B. In need of revision; identity with Madeiran forms uncertain.

Amphorella gracilis (Lowe 1831). P. DG 19c, B 19c on Paiva's authority, provisionally accepted. In need of revision.

FAMILY CLAUSILIIDAE

Boettgeria deltostoma (Lowe 1831). M. F, B. 20c for C and DG. All records of Desertan *Boettgeria* were referred to this species until the work of Neubert and Groh. It appears that all records from B are *B. jensi* (see below).The status of F material from B is uncertain.

Boettgeria jensi Neubert and Groh 1998. 20c for DG and B.

FAMILY HELICIDAE

Heterostoma paupercula (Lowe 1831) M, P. F, DG and B. 20c for C, DG and B. Nearly universal in the Desertas. This is probably an aggregate species, but Desertan specimens have not been studied in detail (see text, p. 4).

Geomitra grabhami (Wollaston 1878) DG only, F and 20c (Groh and Hemmen 1986). Desertan endemic.

Geomitra coronula (Lowe 1852) B only, F. Waldén and Groh and Hemmen (1986) list this as an extant species, without further reference. Wollaston treats it as F only. Desertan endemic.

* *Geomitra tiarella* (Webb and Berthelot 1833) M. F only, DG. (Groh and Hemmen 1986).

* *Spirorbula squalida* (Lowe 1852) M. F on DG only.

[*Caseolus calculus* (Lowe 1854)] P. F on B only on Paiva's authority, rejected.

[*Caseolus compactus* (Lowe 1831)] M, P. B 19c on Paiva's authority, rejected.

Caseolus abjectus (Lowe 1831) M, P. DG & B 20c. The only 19c record for DG is Paiva's; in 20c found only round Doca (site 9) on DG.

[*Caseolus leptostictus* (Lowe 1831)]. M. B 19c, on Paiva's authority, rejected. *C. leptostictus* appears to be confined to the region round Cabo Garajau, M.

Caseolus micromphalus (Lowe 1852). F, DG & B; 20c C, DG & B. A Desertan endemic. Abundant on DG. Not found on B in 1997.

Caseolus punctulatus (Sowerby 1824) P, M (F only). F, B, 20c B. Not found on B in 1997. Absence from C & DG is noteworthy.

[*Disculella spirulina* (Cockerell 1921)] M. B 19c, on Paiva's authority, rejected. *D. spirulina* is restricted to parts of S.W. Madeira.

[*Actinella lentiginosa* (Lowe 1831)]. M. B 19c, on Paiva's authority, rejected. Wollaston omits this from his catalogue.

Actinella actinophora (Lowe 1831). M. DG and B F; DG & B 19c (B on Paiva's authority). Wollaston records a single live specimen from DG. Possible 20c extinction.

[*Actinella arcta* (Lowe 1831)]. M. B 19c on Paiva's authority, rejected. It is possible that this is a misidentification of *A. arcinella* (see below) which is F on DG.

* *Actinella arcinella* (Lowe 1854). M and P (F only). DG, F.

Actinella laciniosa (Lowe 1852). C 20c; DG 19c. Abundant on C. Recorded by Wollaston at north end of DG as a possible introduction from C.

Actinella nitidiuscula (Sowerby 1824) M. DG & B, F. C, DG and B all 20c. Widespread on

all three islands. Subfossil material referred to subspecies *A. n. saxipotens* (Wollaston 1878), much smaller than recent forms.

Discula polymorpha (Lowe 1831). M. F, DG & B. C, DG & B 20c. Widespread and locally abundant on all three islands. There is considerable variation in form between sites on DG, corresponding to subspecies *D. p. poromphala* (Lowe 1852) and *D. p. salebrosa* (Lowe 1862).

Discula tetrica (Lowe 1862). F, B; 19c B on Paiva's authority, accepted. Apparently endemic to B. Wollaston appears confident about the 19c records.

Discula lyelliana (Lowe 1852). DG 19c. Paiva also records it F on DG, rejected by Wollaston, who did not think significant deposits occurred on DG. But Paiva's named locality coincides with site of F deposits. Not found F in 1997. Area (Pedregal) in which it is quoted as moderately common now devoid of vegetation and soil.

[*Cochlicella barbara* (Linnaeus 1758)] non-endemic. B 19c, on Paiva's authority, rejected. Normally associated with dunes and calcareous soils.

Leptaxis erubescens (Lowe 1831) M P. F, DG & B. C, DG 20c, B 19c. Wollaston records it as "swarming" on B, but no 20c records.

Leptaxis vulcania (Lowe 1852). C & DG 20c. F, DG. 19c Paiva records from B are rejected by Wollaston. Waldén regards this as a subspecies of *L. undata* (Lowe 1831), which is Madeiran (see text, p. 4).

Leptaxis leonina (Lowe 1852) DG 19c, B 20c. Recorded by Wollaston in southern part of DG. 20c specimens from that part are juvenile or fragmentary. Waldén regards this as a subspecies of *L. undata* (Lowe 1831), which is Madeiran, and Wollaston hints at clinal variation on DG into *L. vulcania* (see text, p 4).

TWO NEW SPECIES OF *MARCONIA* BOURGUIGNAT, 1889 (GASTROPODA: STREPTAXIDAE) FROM THE ULUGURU MOUNTAINS, MOROGORO DISTRICT, TANZANIA

P. TATTERSFIELD[1]

Abstract   Two new species of Marconia *are described –* Marconia mzinga *and* M. kizinga. *Both species were collected from the same locality in the Uluguru North Forest Reserve, Morogoro District, Tanzania, in sub-montane forest habitat at an altitude of 1250–1500 m asl. The shells of the two species are morphologically very similar but they differ consistently in size without intermediates. Data on the genital anatomy and radula of* M. mzinga *are presented. Options for the generic status of the species and their possible relationships within the Streptaxidae are discussed.*

Key words   Mollusca, Gastropoda, Streptaxidae, Tanzania, Eastern Arc.

INTRODUCTION

This paper describes two new taxa of *Marconia* which were found co-existing in very moist, sub-montane forest on the eastern slopes of the Uluguru mountains, Tanzania. The two taxa are interesting because of their large and consistent difference in size, but otherwise very similar shell morphology. Variation in shell size has been widely reported before in the Streptaxidae although it is usually of a continuous nature within populations. For example, Connolly (1930) describes a collection of *Marconia elgonensis* (Preston) from Mount Elgon which contains shells ranging from 12.4 to 23.5 mm in height, with many intermediates illustrating continuous gradation in size. Van Bruggen (1980, 1985) has discussed population variation in shell size and other characters across the geographical range of some southern African *Gulella* species. Some species examined by van Bruggen display clines whereas others can be separated into subspecies.

Unfortunately, it has only been possible to examine the anatomy and radula of the larger taxon and this presents a problem in deciding how to deal with them. One possibility is that the specimens are representatives of a single species with a large discontinuity in shell size within a population. The other options are to recognise them as two new species or to define a subspecies to account for the size variation. However, in view of their sympatric distribution the subspecies option does not seem appropriate so I have therefore decided to describe two new species.

The Ulugurus are a range of Precambrian, crystalline, basement rock mountains that lie to the south of the town of Morogoro in north-east Tanzania; their rocks form part of the Mozambique Belt. The range was formed by block faulting processes, which probably started during the Karroo (290–180 myr BP) although the present day range probably developed during the Neogene and more recently with the formation of the East African Rift System (7–0 myr BP) (Griffiths, 1993).

The Uluguru Mountains are part of the Eastern Arc chain, which extends as a series of isolated massifs from the Taita Hills in south-east Kenya through eastern Tanzania to the Udzungwa mountains in southern Tanzania. Lovett (1990) has defined Eastern Arc Mountains as those under the direct climatic influence of the Indian Ocean. The Eastern Arc mountains receive a high rainfall from moist air from the Indian Ocean and parts of the eastern slopes of the Ulugurus are under an almost perhumid climate. There is evidence that the Indian Ocean has been relatively stable during the Pleistocene

[1] Department of Biodiversity and Systematic Biology, National Museum of Wales, Cathays Park, Cardiff CF1 3NP, UK.
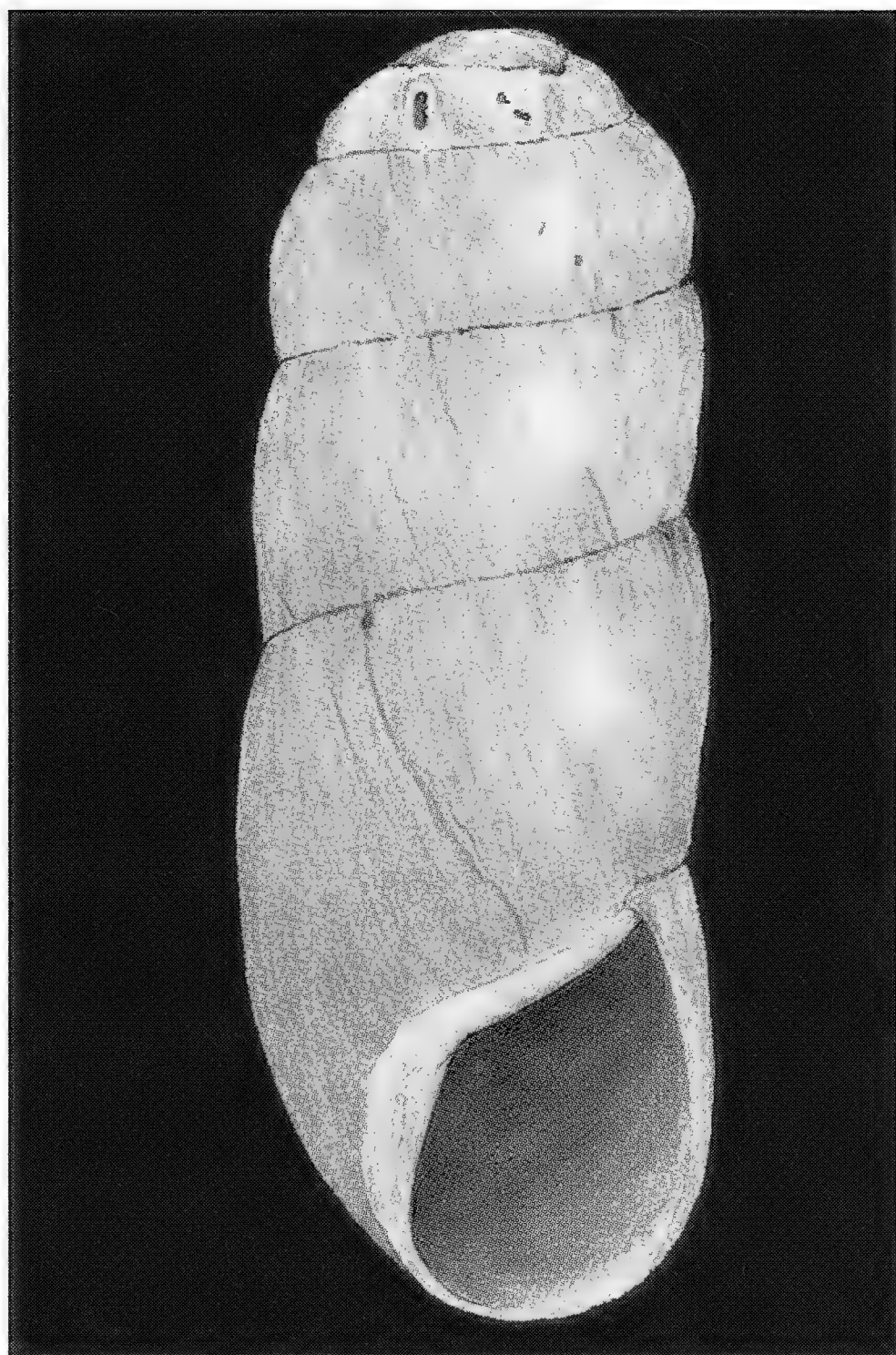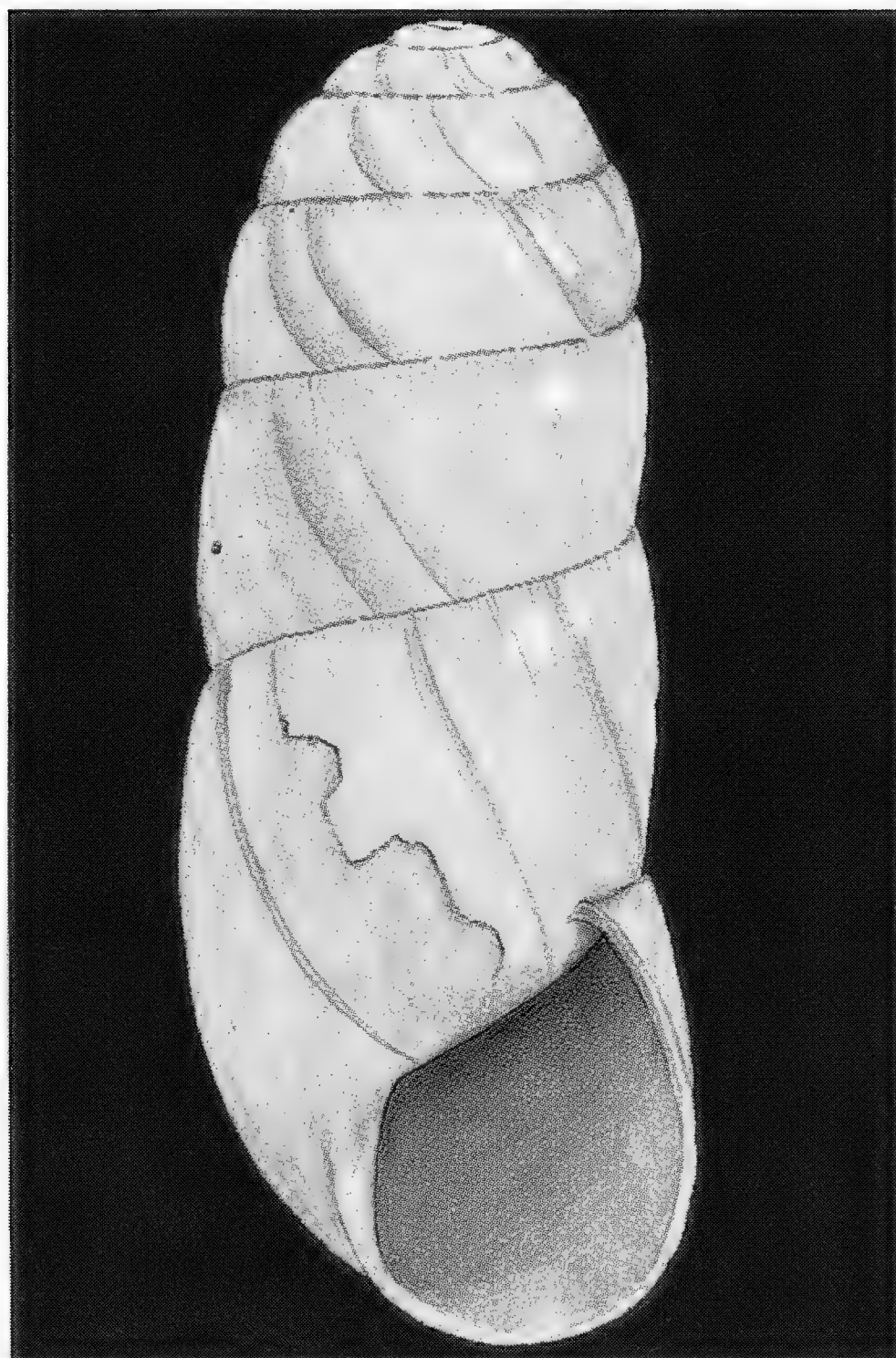
Fig. 1 Holotype shell of *Marconia mzinga* n. sp. **Fig. 2** Holotype shell of *Marconia kizinga* n. sp.
H=14.7mm   H=8.6mm

(Hawthorne, 1993) and it has therefore been supposed that at least some areas of these mountains may have continuously supported moist forests over very long time spans.

The biota of the Eastern Arc mountains is characterised by a large number of range-restricted species in many animal and plant groups (see papers in Lovett and Wasser, 1993; Rodgers and Homewood, 1982). Their mollusc faunas are still poorly known but those of the Usambara mountains, which lie to the north of the Ulugurus, are reported to have a molluscan endemism rate of at least 42% (Rodgers and Homewood, 1982).

The following abbreviations for shell dimensions are used:

H   Shell height
D (W)   Maximum shell diameter measured to the outer edge of the aperture, which is inflated and extends beyond the otherwise uniform outline of the shell in adult specimens.
D (S)   Shell diameter   excluding inflated aperture.
h   Aperture height measured to the outer edge of the thin white callus on the parietal and columellar zones.
d   Aperture diameter

Abbreviations for museums are as follows:
AMNH American Museum of Natural History, New York, USA
BMNH Natural History Museum, London, UK
NMK   National Museum of Kenya, Nairobi, Kenya
NMT   National Museum of Tanzania, Dar es Salaam, Tanzania
NMW   National Museum of Wales, Cardiff, UK
RMNH National Museum of Natural History, Leiden, Netherlands

TABLE 1
Shell dimensions (mm) of a selection of *Marconia mzinga* n.sp.

H	D (W)	D (S)	h	d	Whorls	H/D(s)	Notes
Holotype							
14.7	5.8	5.2	5.0	3.8	7.00	2.8	Adult
Paratypes							
15.9	6.3	5.2	5.2	4.4	7.25	3.0	Adult
18.6	6.6	5.5	5.8	4.7	8.13	3.4	Adult
16.5	Broken	5.2	5.7	4.2	7.00	3.2	Adult
15.7	5.9	5.0	5.0	4.0	6.75	3.1	Adult
15.6	5.7	5.3	5.0	4.3	7.50	2.9	Adult
15.4	5.2	4.9	5.1	3.8	7.00	3.2	Adult
15.3	5.0	5.7	4.9	4.0	7.00	2.7	Adult
15.3	5.7	4.9	5.0	4.0	7.00	3.1	Adult
15.1	4.8	5.6	4.7	3.5	7.00	2.7	Adult
15.0	5.1	5.4	5.0	3.9	6.75	2.8	Adult
15.0	5.7	5.1	4.7	4.1	6.75	2.9	Adult
14.8	5.6	5.0	5.0	3.8	7.00	3.0	Adult
14.6	5.4	4.8	4.9	4.1	6.50	3.1	Adult
14.6	5.7	4.8	4.9	4.1	6.50	3.1	Adult
14.5	5.4	4.9	4.7	3.7	6.75	3.0	Adult
14.3	5.5	5.0	5.0	4.0	7.00	2.8	Adult
14.2	4.9	5.0	4.8	3.8	7.00	2.9	Adult
14.2	Obscured	5.0	Obscured	Obscured	7.00	2.9	Adult
14.1	5.6	4.9	4.8	4.0	6.50	2.9	Adult
13.9	4.8	5.3	4.7	3.7	7.00	2.6	Adult
13.9	5.2	4.8	4.4	3.9	7.00	2.9	Adult
13.9	5.2	4.8	4.8	3.9	7.00	2.9	Adult
13.8	5.3	4.8	4.5	3.7	6.50	2.9	Adult
13.7	5.3	4.9	4.9	3.8	6.50	2.8	Adult
13.7	5.3	4.7	4.5	4.0	6.50	2.9	Adult
13.7	5.5	4.8	4.5	3.7	6.25	2.9	Adult
13.7	5.0	4.9	4.7	4.0	6.75	2.8	Adult
13.7	5.0	4.6	4.2	3.7	6.50	3.0	Adult
13.7	5.5	5.0	4.7	4.0	6.50	2.7	Adult
13.6	4.9	4.9	4.7	3.8	7.00	2.8	Adult
13.6	5.4	5.0	4.4	4.1	6.25	2.7	Adult
13.5	5.6	4.8	4.5	3.7	6.50	2.8	Adult
13.1	5.7	5.0	4.8	4.0	6.00	2.6	Adult
13.0	4.7	5.2	4.7	3.7	6.75	2.5	Adult
12.2	4.9	4.7	4.7	3.5	5.75	2.6	Adult
11.6	5.1	4.4	4.4	3.5	5.75	2.7	Adult?
11.3	5.0	4.9	4.4	3.0	6.00	2.3	Juvenile
10.6	5.0	4.9	4.6	3.0	6.13	2.2	Juvenile
10.1	4.7	4.7	4.4	2.6	5.50	2.1	Juvenile
9.9	4.9	4.8	4.0	2.7	5.75	2.1	Juvenile
9.7	4.7	4.6	3.8	3.0	5.50	2.1	Juvenile
9.6	4.7	4.7	4.0	2.8	6.00	2.0	Juvenile
9.3	4.7	4.7	3.8	3.0	6.00	2.0	Juvenile
9.1	4.7	4.7	3.9	2.9	5.75	1.9	Juvenile
8.7	4.6	4.6	3.8	2.8	5.50	1.9	Juvenile
6.9	4.3	4.3	3.4	2.6	4.75	1.6	Juvenile
5.7	4.4	4.4	2.9	2.4	5.33	1.3	Juvenile
5.7	4.6	4.5	3.1	1.9	5.00	1.3	Juvenile
2.8	3.6	3.6	1.7	1.7	3.13	0.8	Juvenile*
2.6	3.7	3.7	1.9	1.7	3.00	0.7	Juvenile*
2.3	3.5	3.5	1.4	1.5	2.75	0.6	Juvenile*

*Juvenile with umbilicus

SYSTEMATIC DESCRIPTIONS

STREPTAXIDAE

Genus *Marconia* Bourguignat 1889
Marconia mzinga n. sp.
Fig. 1

Holotype   1sh collected by P. Tattersfield, January 1996, by direct searching forest floor leaf litter. NMW.Z.1996.148.

Paratypes   Many adult and sub-adult sh. and live specs. preserved in ethanol, as Holotype, NMW.Z.1996.148 and RMNH, NMT, NMK, BMNH, AMNH.

Shell Measurements   See Table 1.

Type Locality   Uluguru North Forest Reserve, Uluguru Mountains, Morogoro District, Morogoro Region, Tanzania. All specimens were collected from leaf litter in submontane forest on the east side of the Uluguru range, above Tegetero Mission. Altitude *c.*1250–1500 m asl. Location: 6.935 S 37.685 E.

The Forest Reserve covers the steep summit ridge and easterly slopes of the northern half of Uluguru Mountains between Morogoro town and the Mgeta - Bunduki depression. Lovett and Pócs (1993) list tree species present in the Forest Reserve and describe
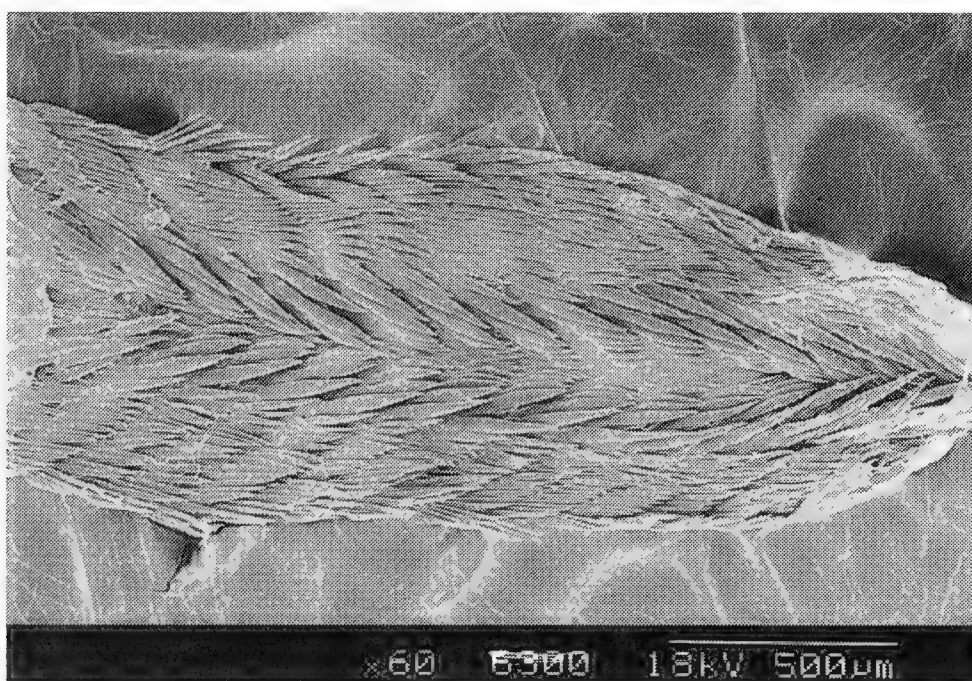

Fig. 3a Radula of *Marconia mzinga* n. sp.

Fig. 3b Radula of *Marconia mzinga* n. sp. showing central tooth and six lateral teeth.
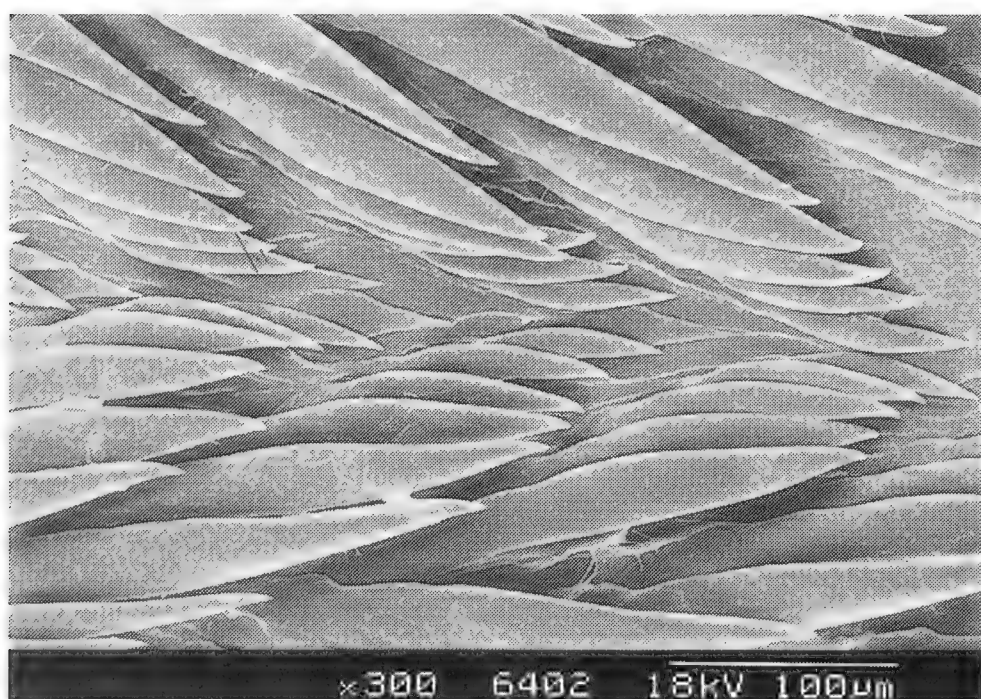
Fig. 3c Outer part of radula of *Marconia mzinga* n. sp. showing 15–16 marginal teeth.

Penial retractor
muscle with
accessory retractors

Hermaphrodite
duct

Spermatheca

Epiphalloid sac with
armature

Large penial
hooks showing
through wall

Vas deferens

Penis

0   1   2

Scale in mm
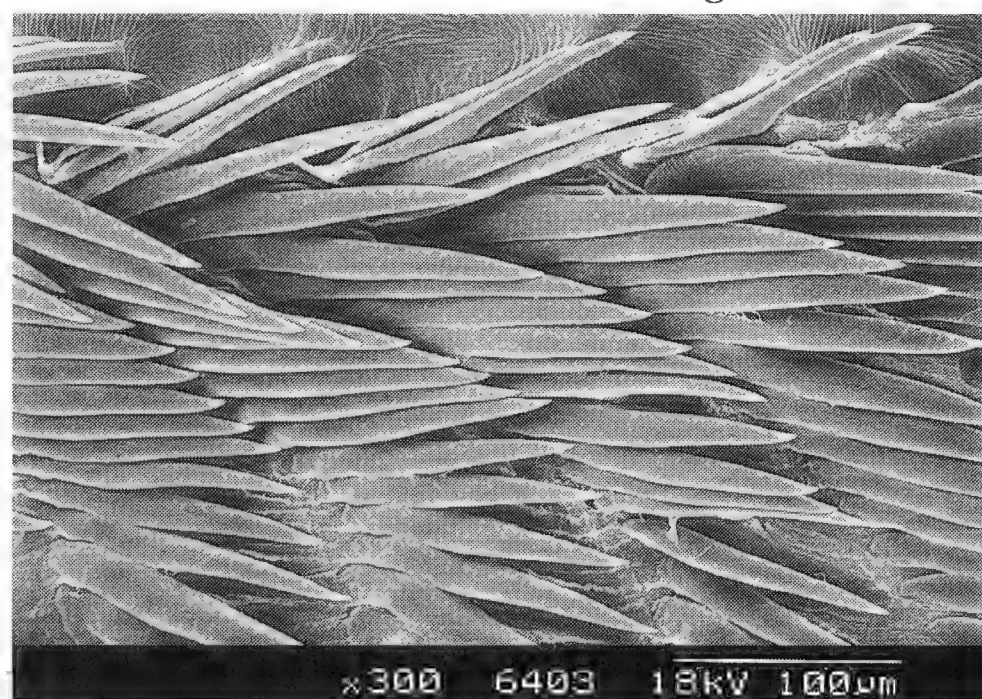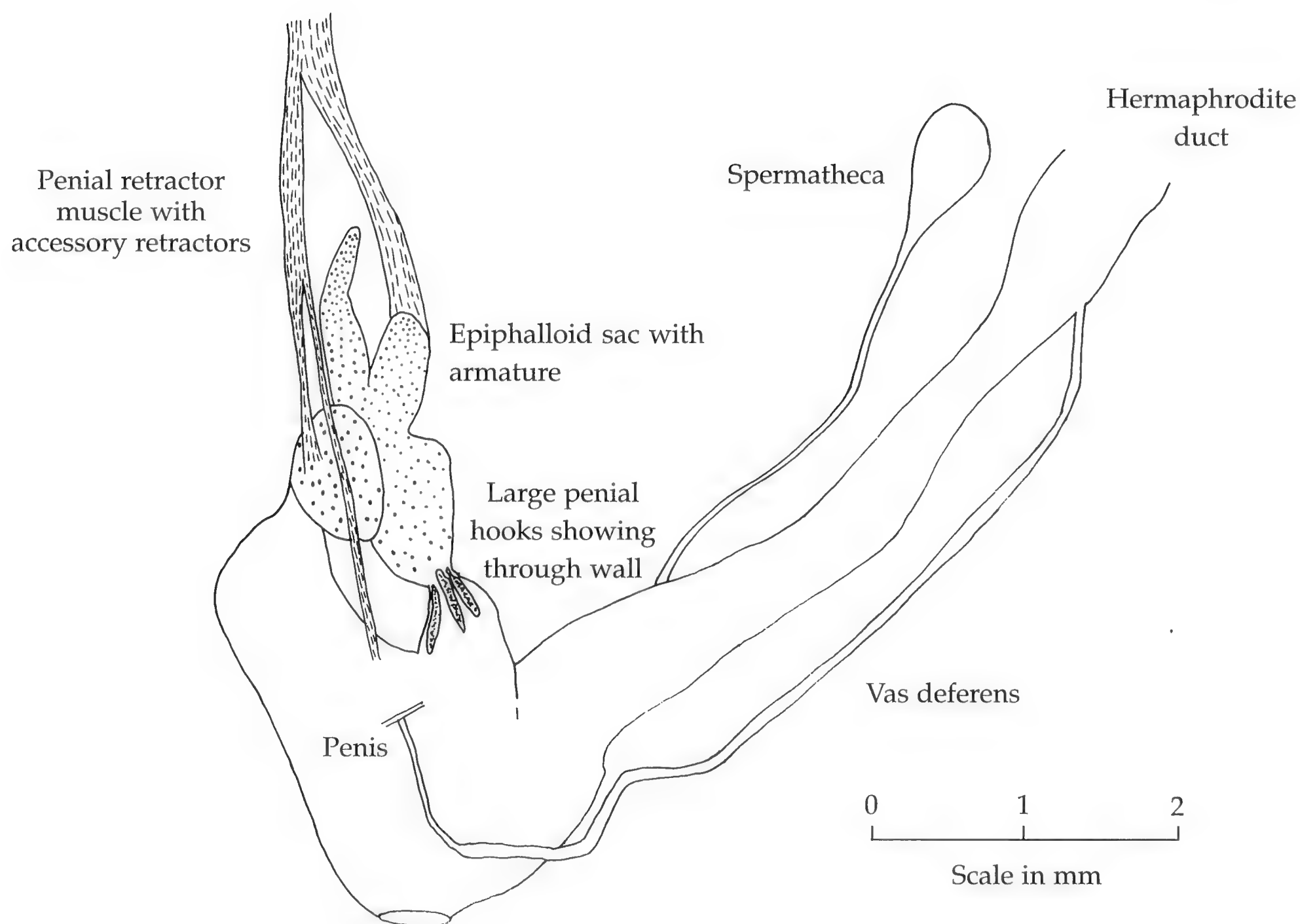
Fig. 4 Genital anatomy of *Marconia mzinga* n. sp.

the soils as acidic lithosols with ferralitic red, yellow and brown latosols which have developed over Precambrian granulite, gneiss and migmatite rocks. They estimate rainfall as 2900–4000 mm/year on the eastern slopes of the Reserve, without a marked dry season. In the areas of collection the forest canopy was typically tall (*c*.30–50 m) with many large trees densely covered by epiphytic ferns, mosses, the giant nest fern *Asplenium nidus* and other plants. The surrounding topography was strongly undulating with small valleys, ridges and steep slopes.

Description   Holotype shell 14.7 mm high (Table 1), elongated cylindrical with a very slight taper from the base of the shell to the domed apex; smooth, glossy, very pale yellowish-brown. In adult shells, the outer margin of the aperture is expanded away from the axis so that the cylindrical outline of the shell is slightly distorted; juvenile shells do not have such an expanded aperture and are consequently more perfectly cylindrical. The last whorl is relatively large, contributing about 60% of the height of the shell. The apical whorls have a very faint, regular, spiral microsculpture that is only visible under high magnification. Lower on the shell, there are occasional, widely and irregularly spaced, oblique, radial lines probably reflecting periods of arrested growth. Whorls 7. Suture weakly crenellate or beaded, especially between upper whorls. Umbilicus closed in adult but open in juveniles of about 3¼ whorls or less. Aperture pyriform and edentate. Apertural lip blunt, weakly thickened especially near junction of basal and columellar areas, but not reflected, not fragile. Peristome discontinuous across parietal region. The internal shell mouth is white with a very thin, white, callus extending across the parietal and columellar regions.

The feeding apparatus is large and occupies most of the body from the head to the front of the mantle flap. The radula (Fig. 3a) is about 6 mm long with 50 rows of teeth. There are six lateral teeth on each side (Fig. 3b), which enlarge rapidly from the small

tooth bordering the centre of the radula, to the 5th and 6th which are the largest. There is a central tooth present in some specimens but it is obscured or possibly absent in others. There are 15–16 short, sub-equal marginals (Fig. 3c).

The body, sole and tentacles of the animal (preserved in 70% ethanol) are uniform creamy yellow. The genital opening is located on the upper, right-hand side of the body, at the edge of, or just beneath the mantle flap.

The genital structure (Fig. 4) has a complicated epiphalloid sac at the proximal end of the penis, with one or more lobes or extensions. The main retractor muscle attaches to a proximal lobe on the epiphalloid sac, but there are two further accessory retractor muscles that join to the penial structure near the junction of the penis and sac. Internally, the wall of the epiphalloid sac is armoured with a large number or hard, reddish brown hooks (Fig. 5), which are visible from the outside through the rather thin wall of the sac. Six of the hooks near the junction of the sac and penis are distinctly larger (length approximately 0.3 mm) than the rest; these have elongated bases and are visible as short
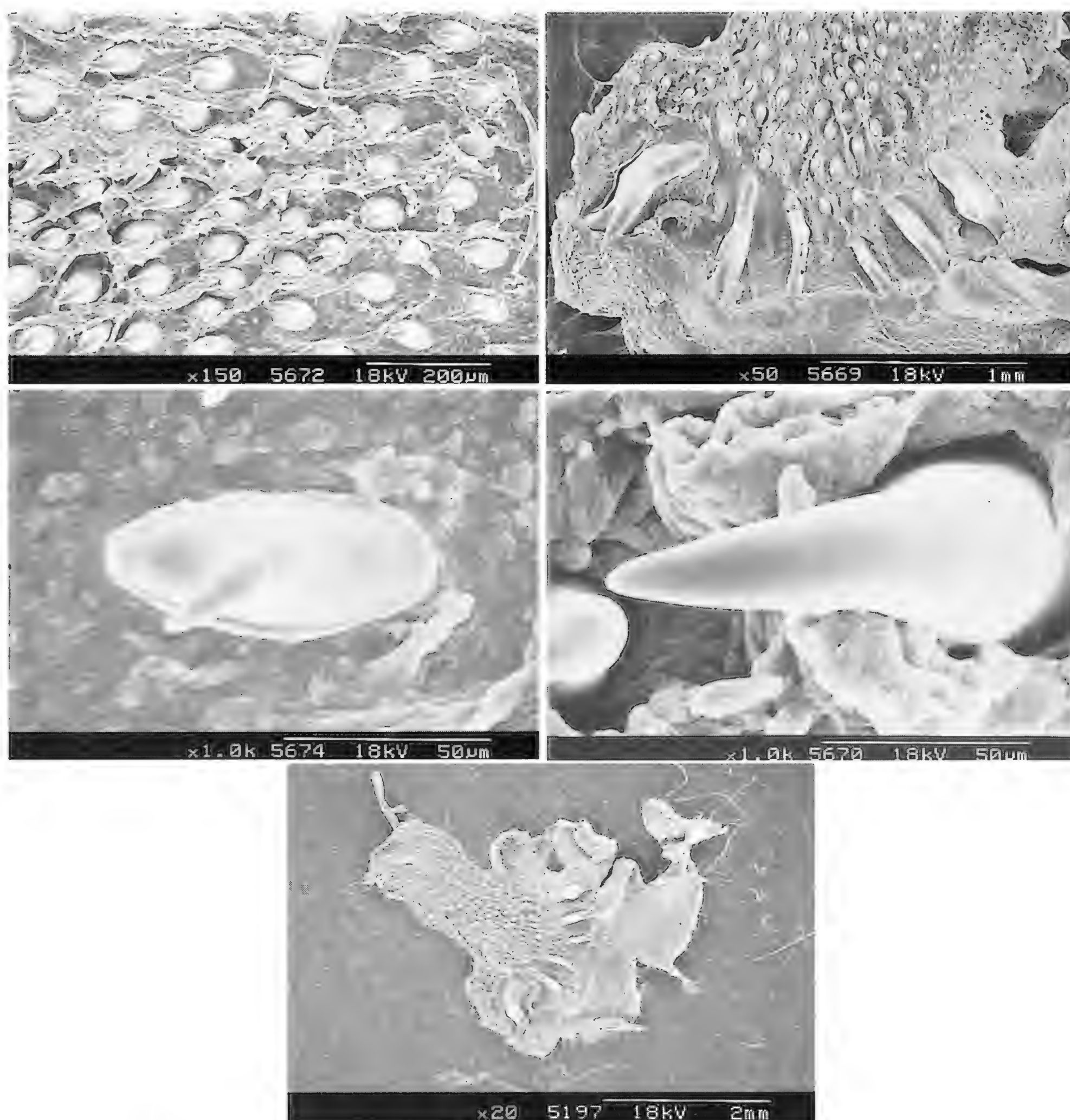
Fig. 5   SEM showing internal penial armature of *Marconia mzinga* n. sp.
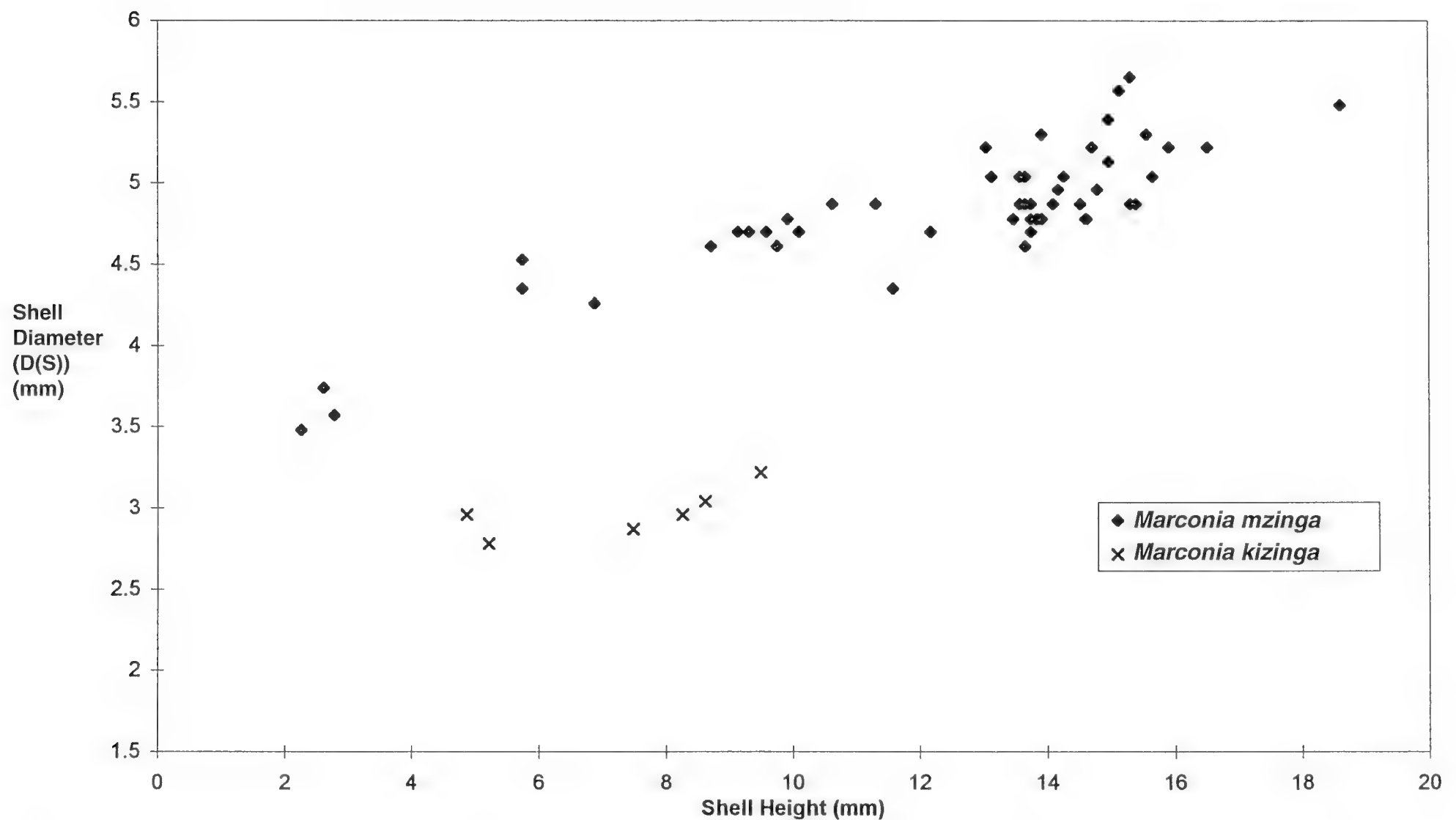
Fig. 6 Shell diameter (D(S)) against shell height for *Marconia mzinga* n. sp. and *Marconia kizinga* n. sp.

dark stripes through the sac wall. The remaining hooks are smallest at the proximal end of the sac and gradually increase in size towards the junction with the penis; they are visible as nearly circular or slightly elongated reddish dots through the wall of the sac. The wall of the penis is thickened.

Derivation of name   an African beehive or cannon (swahili).

Comparisons   The shell closely resembles *Stenomarconia jeanneli* (Germain, 1934) in size, shape and general form, but that species differs in its dark, olive-green colour, lightly reflected peristome and its absence of spiral microsulpture (Germain, 1934). Verdcourt (1961) describes and figures the genital anatomy of *Stenomarconia jeanneli* but does not mention internal penial armature of hooks or the triple retractor muscle arrangement found in *Marconia mzinga*. The structure of the penial complex of *S. jeanneli* is also different, being divided in the middle into two parts - a long narrow, clavate appendage and the main part with vas deferens and retractor muscle given off at the extreme apex (Verdcourt, 1961). In *Marconia mzinga*, the vas deferens arises lower down on the penial complex. Like *Marconia mzinga*, the radula of *S. jeanneli* has about 21–22 teeth per half row with one maximum, the sixth tooth being the largest (Verdcourt, 1961). However, it lacks a central tooth (although this character may not be diagnostic) and the 6 outer-most teeth are narrower than the rest. *Stenomarconia* was erected as a subgenus by Germain but was promoted to generic rank by Verdcourt (1961) on the basis of its anatomy, shell colour (which is very unusual in the family) supported by its distinctive ecology. It is a monotypic genus known only from moorland and forest habitats at high altitude (3300–4000m) on Mount Kenya.

Several other edentate, cylindrical streptaxids have been described from East Africa. *Gulella rectangularis* (Preston), (Urguess, northern Kenya), *Marconia masabana* Connolly, (Mount Elgon, Uganda, 7000–9000 ft), and *Gonaxis cylindrica* (K L Pfeiffer) are all smaller and differ in their more quadrate shell apertures, relatively smaller body whorl in proportion to the remainder of the shell and reflexed peristomes. *Marconia masabana* also differs in its radula which has 19 or 20 teeth in each half row, lacks a central tooth with

the 5th tooth being the largest and the 19th much smaller than the rest (Connolly, 1930). The species is larger but otherwise conchologically similar to *Marconia mzinga* (see below).

The generic assignment of this species is discussed below.

Marconia kizinga n. sp.
Fig. 2

Holotype   1 sh. collected by P. Tattersfield in January 1996, by direct searching leaf litter, NMW.Z. 1996.148.

Paratypes   3 adult sh. plus 3 sub-adult sh., as Holotype, NMW.1996.148, RMNH, NMT.

Shell Measurements   Table 2

Type Locality   Uluguru North Forest Reserve, Uluguru Mountains, Morogoro District, Morogoro Region, Tanzania. All specimens were collected from leaf litter in sub-montane forest on the east side of the Uluguru range, above Tegetero Mission, Altitude *c*.1250–1500 m asl. Location: 6.935 S 37.685 E. Other details of type locality as for *Marconia mzinga*, with which this species was found living.

Description   Holotype shell (Table 2) 8.6 mm high. Elongated cylindrical with domed apex. Cream or yellowish white. Shell surface smooth or locally with weak and irregular radial growth lines. The apical surface of the holotype is corroded and lacks a periostracum, but very faint spiral microsculpture is visible on the apical whorls of a juvenile paratype that is in better condition. Whorls $5\frac{1}{4}$. The last whorl contributes approximately 60% of the total shell height. The holotype has two radial lines, possibly indicating periods of arrested growth, one being wider that the other and being distinguished by a darker band of shell. Anatomy and radula unknown.

Suture very weakly crenellate. Umbilicus closed in adult. Aperture pyriform and edentate. Apertural lip blunt, weakly thickened especially near junction of basal and columellar areas, but not fragile or reflected. Peristome discontinuous across parietal region. There is a very sparse, thin, white, callus extending across the parietal and columellar regions.

TABLE 2
Shell dimensions (mm) of *Marconia kizinga* n. sp.

H	D (W)	D (S)	h	d	Whorls	H/D(s)	Notes
Holotype							
8.6	3.3	3.0	3.0	2.4	5.25	2.8	Adult
Paratypes							
9.5	3.3	3.2	3.1	2.4	5.5	2.9	Adult
8.3	3.4	3.0	2.8	2.4	5.5	2.8	Adult
7.5	3.1	2.9	2.8	2.0	5.5	2.6	Adult
5.2	2.9	2.8	2.3	2.6	4.5	1.9	Juvenile
4.9	3.0	3.0	2.1	1.7	4.25	1.6	Juvenile

Note: one further juvenile shell too broken to measure

Derivation of name   a small African beehive or cannon (ki- prefix = small (swahili)).

Comparisons   Apart from the smaller size of the shell, this species bears a close similarity to *Marconia mzinga*. Plots of H against D(S), and whorl number against D(S) (Figs. 6 and 8) clearly show that the two species can be readily separated using shell size and
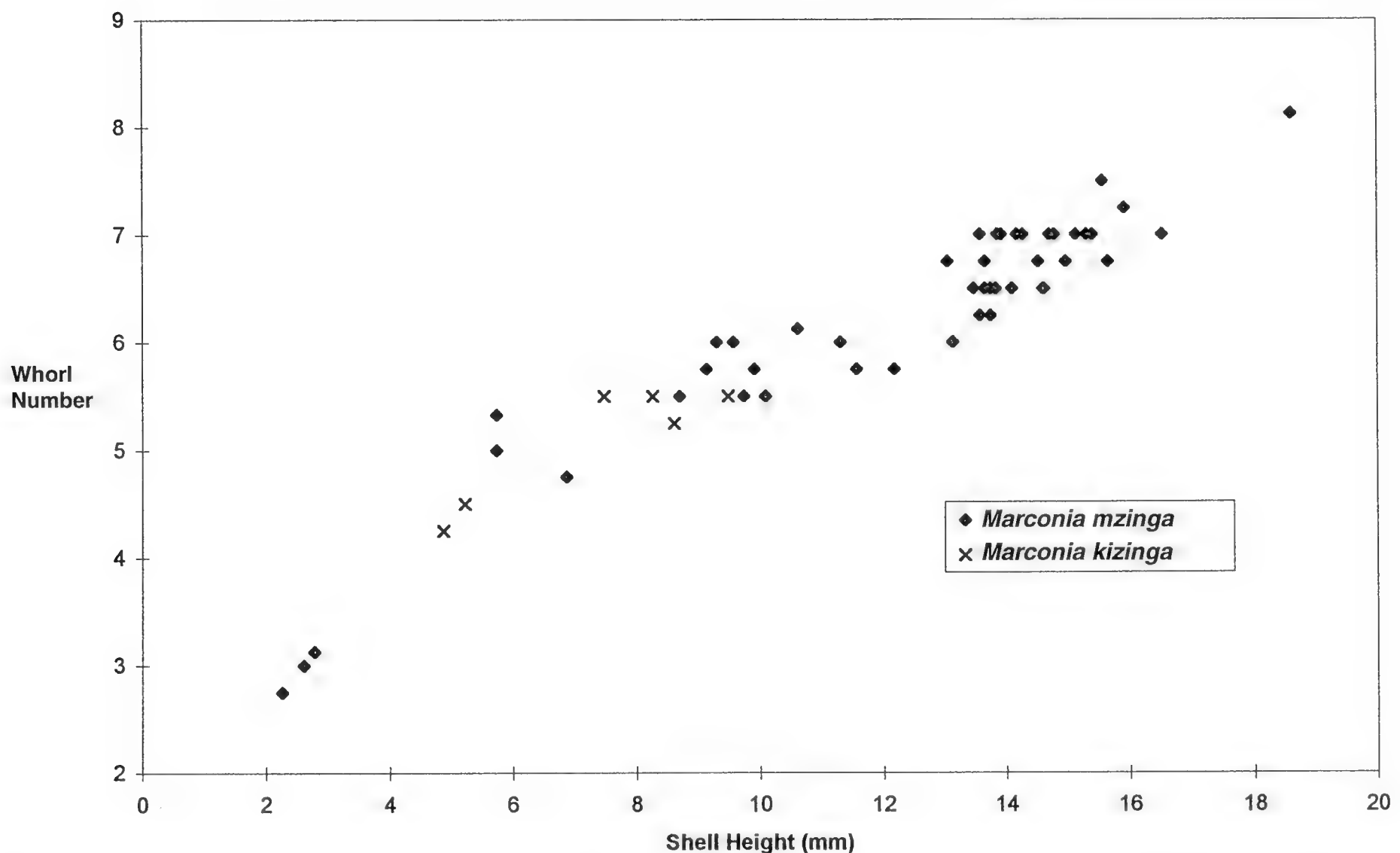
Fig. 7 Whorl number against shell height for *Marconia mzinga* n. sp. and *Marconia kizinga* n. sp.

that the collection does not include any material of intermediate size. *Marconia kizinga* has a consistently more slender shell than *Marconia mzinga*, irrespective of shell height. However, both species have the same number of whorls for a given shell height (Fig. 7).

As with *M. mzinga*, comparison with the other cylindrical, edentate streptaxids is appropriate. This species is closer to *Gulella rectangularis* (Preston) and *Gonaxis cylindrica* (K. L. Pfeiffer) in respect of shell size, but these, and the other species discussed above, can be excluded on the grounds of shell colour and size (*Stenomarconia jeanneli*), and reflexed apertural lip (*Gulella rectangularis*, *Gonaxis cylindrica* and *Marconia masabana*).

This species is clearly closely related to *Marconia mzinga* and its generic assignment is discussed below.

GENERIC ASSIGNMENT OF NEW SPECIES

Several authors (eg. Thiele, 1931; Pilsbry, 1919) have attempted to clarify the systematic position of *Gonaxis* and other Streptaxinae, placing different emphasis on shell, radula and anatomical characters. However, as yet it is clear that there is insufficient information available, especially on soft anatomy and radula, to form a fully satisfactory definition of these or indeed most other streptaxid genera. Pilsbry (1919) acknowledged this problem in the Streptaxinae for *Edentulina*, *Eustreptaxis*, *Marconia* and *Gonaxis*, noting that 'while there is no difficulty in assorting the species and the extreme forms of each are conspicuously unlike, it is not easy to see where generic lines are to be drawn'. Accordingly, Pilsbry decided to adopt a purely working arrangement, placing conspicuously distorted forms in *Gonaxis* and leaving *Edentulina* and *Marconia* as genera. In view of this, it is clear that the generic assignment of these new streptaxids is to a degree arbitrary. However, there would appear to be four options - *Gulella*, *Stenomarconia*, *Gonaxis* or *Marconia*.

The shells of both *mzinga* and *kizinga* superficially resemble an edentate *Gulella*, but I do not favour this option because most *Gulella* species have a strengthened and reflected
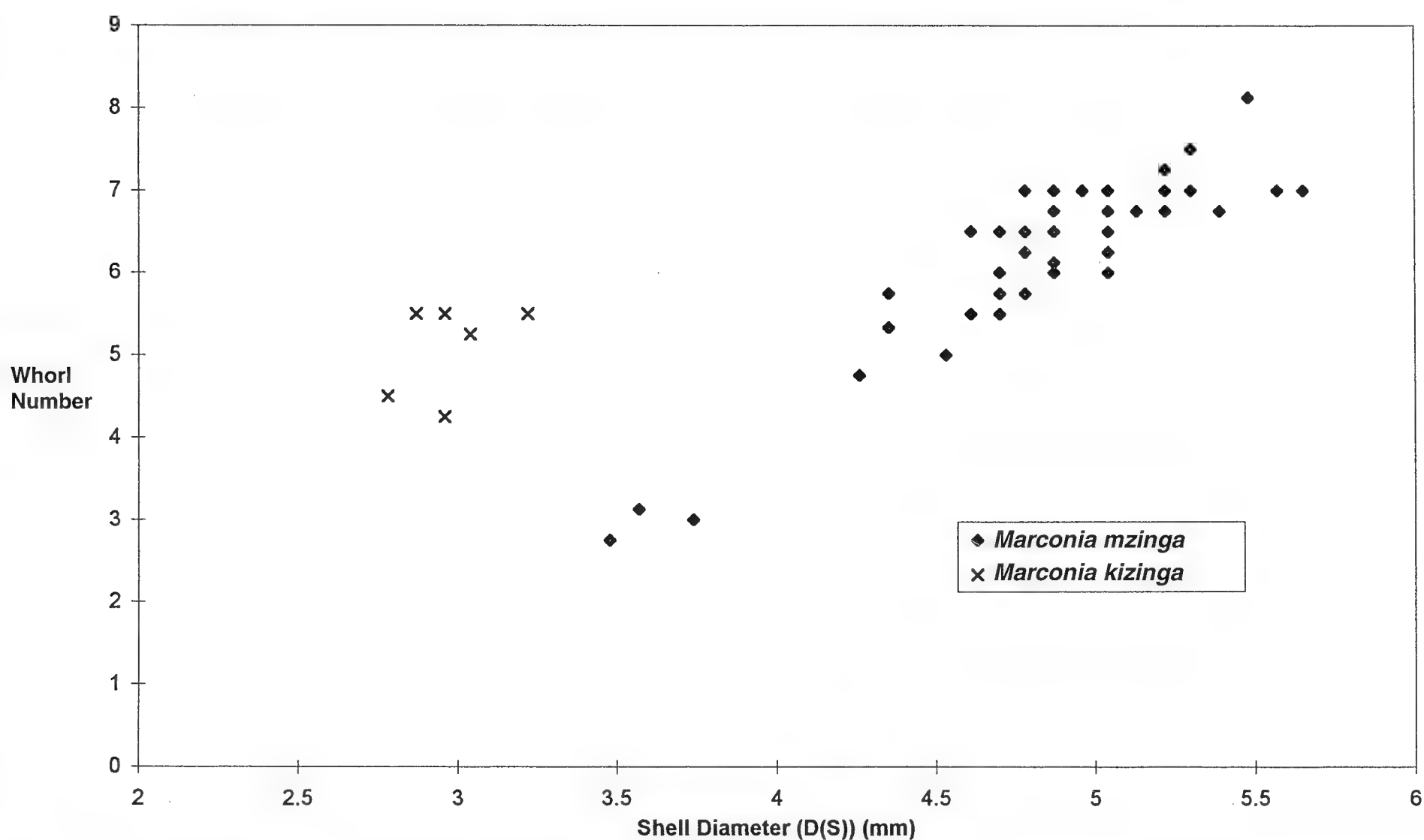
Fig. 8   Whorl number against shell diameter for *Marconia mzinga* n. sp. and *Marconia kizinga* n. sp.

peristome and do not have such a large body whorl in proportion to the rest of the shell. Based on the relatively long axis of the shell, these species might be placed in the sub-family Ptychotrematinae, which includes *Gulella*, but as Pilsbry (1919) notes, such shell characters are rather trivial and it seems to me clear that they belong in the Streptaxinae.

Interpretation of the taxa *Marconia* and *Gonaxis* has been the subject of much debate and argument (Bequaert and Clench, 1936; Pilsbry, 1919; Adam, 1965; Verdcourt, 1961, 1966) and still has not been resolved at all satisfactorily. Bourguignat (1889) introduced *Marconia*, and Pilsbry (1919) and Thiele (1931) considered Bouguignat's *M. gibbosa* to be the genotype. Later, Bequaert and Clench (1936) pointed out that the genotype of *Marconia* is *Ennea lata* as selected by Kobelt (1906). Gude (1902) included the taxon in *Streptaxis*, noted that the epithet *gibbosa* was not available since it had been used by Pfeiffer and accordingly renamed the species *marconi*; however, this approach does not seem to have been accepted by most subsequent authors (but see Richardson, 1986).

Pilsbry (1919) decided to retain generic rank for *Marconia* on the basis of the unusual radula of *M. lata ruwenzoriensis* Pilsbry which has two maxima in the lateral teeth (Pilsbry, 1919). However, according to Adam (1965), the radula of *M. lata* (from an unspecified location and without a figure) does not have such a double maximum; Verdcourt (1961) noted that the radula of *M. gibbosa* has only one maximum (Verdcourt, 1961). There is thus some contradiction or at best ambiguity over the radula of *M. lata*, and an apparent difference in the main radula character between Bourguignat's *M. gibbosa* and *M. lata ruwenzoriensis*. It would thus seem unwise to place too much emphasis on these characters, at least until more material, ideally from type localities, has been examined.

Bequaert and Clench (1936) also noted the problems with radula characters and adopted a primarily conchological classification in which *Marconia* was retained at generic rank for 'shortly cylindric species, showing no distortion of the shell, and with very obtuse dome-like summit'. They used *Gonaxis* for species with a 'more or less distorted spire, the body whorl being shifted to one side of the axis'. However, they also noted that 'no sharp line of demarcation can be drawn between *Marconia* and *Gonaxis* on shell character alone' and placed *gibbosa* in *Gonaxis* because of its asymmetrical shell.

Verdcourt (1961, 1966) seems to have followed Pilsbry's emphasis on the number of maxima on the radula and assigned species to two sub-genera of *Gonaxis* - *Gonaxis* subgenus *Gonaxis* (= *Marconia* Bourguignat) and *Gonaxis* subgenus *novum*, although a new sub-genus has as yet not been formally erected. However, the diagnostic characters for each of these taxa are not fully clear.

Several authors have considered anatomical characters, especially of the gentialia but at present there would appear to be little consistency which assists in delineation of the taxa. Distinctive penial hooks similar to those present in *mzinga* have been described in *Gonaxis enneoides* (von Martens) by Adam (1965), but their use as generic or subgeneric characters has not been explored further in streptaxids to my knowledge. The shell shape and radula of *Gonaxis enneoides* are different from *M. mzinga*.

Germain (1934) originally designated *Stenomarconia* as a section of *Marconia*, stressing its narrowly cylindric shell shape, lightly reflected peristome and colour, which he described as 'magnifique vert olive teinté de marron'. Verdcourt (1961) also placed emphasis on the dark shell colouration that is very unusual in the Streptaxidae, as well as anatomy and habitat, when promoting *Stenomarconia* to generic status. Shell colour and habitat would not generally be considered robust characters for the delineation of a pulmonate genus although useful characters are clearly difficult to define since the 'group' is monotypic. The shell shape of both of these new species and the radula of *M. mzinga* are similar to *Stenomarconia jeanneli*, although there are differences in the characters emphasised by Verdcourt (1961).

The above discussion clearly illustrates the extent to which the genera concerned are still poorly defined. No suite of characters has been identified which can adequately delineate them and thus none of the generic options is fully satisfactory. Assignment to *Stenomarconia* (at either generic or sub-generic level) would seem to be reasonable based on conchological characters, but in my view this is outweighed by the differences in other aspects, including the distinct ecology and colour of Germain's species. Furthermore, a more detailed exploration of the anatomy of *Stenomarconia* would be desirable (especially on retractor muscles and penial armature) before risking adding potential confusion to what currently stands out as being a rather distinctive genus, albeit mainly only on the grounds of colour and habitat.

For the reasons discussed above, neither *Gonaxis* nor *Gulella* would appear to be satisfactory. I have therefore decided to adopt an entirely pragmatic solution and have assigned the new species to *Marconia*. However, I acknowledge that there are several problems associated with this approach and that re-assignment will probably be necessary when more complete data allow a better definition of the genera concerned.

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The British Ecological Society, Linnean Society and the Peoples Trust for Endangered Species generously supported the fieldwork.

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DISTRIBUTION AND CONSERVATION STATUS OF *PERFORATELLA RUBIGINOSA* (PULMONATA: HELICIDAE) IN BRITAIN

I.J. KILLEEN[1]

Abstract   In 1995 a survey was undertaken on behalf of the statutory conservation agency, English Nature as part of their Species Recovery Programme to determine the status of the known populations of Perforatella rubiginosa *in England and to identify other populations within the known range.*

The results demonstrated that P. rubiginosa *was thriving at all of its known British sites which lie in the Thames basin, except Burham, Kent where only dead shells were found. Many of the populations are large and are more extensive than previously recognized. In addition, it was also found on Brentford Ait East, representing a new site for the species.*

In Britain, P. rubiginosa *is demanding in its habitat requirements. Most sites are within the flood zone of tidal freshwater rivers and are characterized by having areas of bare mud vegetated by tall herbs. Flood rubbish such as planks, logs, dead stems and plastic is a feature at all sites and represents an important refuge for the snail. Most sites are relatively sheltered and would be gently lapped by a significant proportion of high tides.*

The restricted nature and extent of the habitat at all sites means that all populations are vulnerable. The principal threats come from industrial and urban development; inhibition of the tidal action by piling, barrages or locks and over-management such as clearance of the flood rubbish.

Key words   Perforatella, Distribution, Conservation status.

INTRODUCTION

The British Red Data Book (Bratton 1991) lists thirty-three species of terrestrial, freshwater or brackish-water molluscs. In this list, *Perforatella rubiginosa* (A. Schmidt, 1853) is classified under Category RDB2, Vulnerable. However, it is not included on the UK Biodiversity Action Plan Short-list (HMSO 1996). The nomenclatural problems with this species have been discussed by Falkner (1993) who has placed it in the genus *Pseudotrichia*. However, to avoid confusion, *Perforatella*, is the name used throughout this paper.

Perforatella rubiginosa, sometimes known (in the UK) as the German Hairy Snail, was first recognized in Britain in 1981 (Verdcourt 1982) although specimens recorded by Quick (1960) as *Trichia plebeia* (Draparnaud, 1805) from a Thames-side site at Pangbourne were later shown to be *P. rubiginosa* (see Naggs 1983). By 1994 it was known from eight sites in England, all of which were along the River Thames or rivers flowing into the Thames estuary. Many of these sites had not been examined since the snail was first recorded.

The status of *Perforatella rubiginosa* as a native British species is uncertain. Specimens originally assigned to this species from Pleistocene deposits in Norfolk were later disproved (Naggs 1983). The only undisputed fossil specimens are from a Late Bronze Age excavation at Runneymede (Evans 1987). Thus it would appear that *Perforatella* is a

[1] Malacological Services, 163 High Road West, Felixstowe, Suffolk IP11 9BD
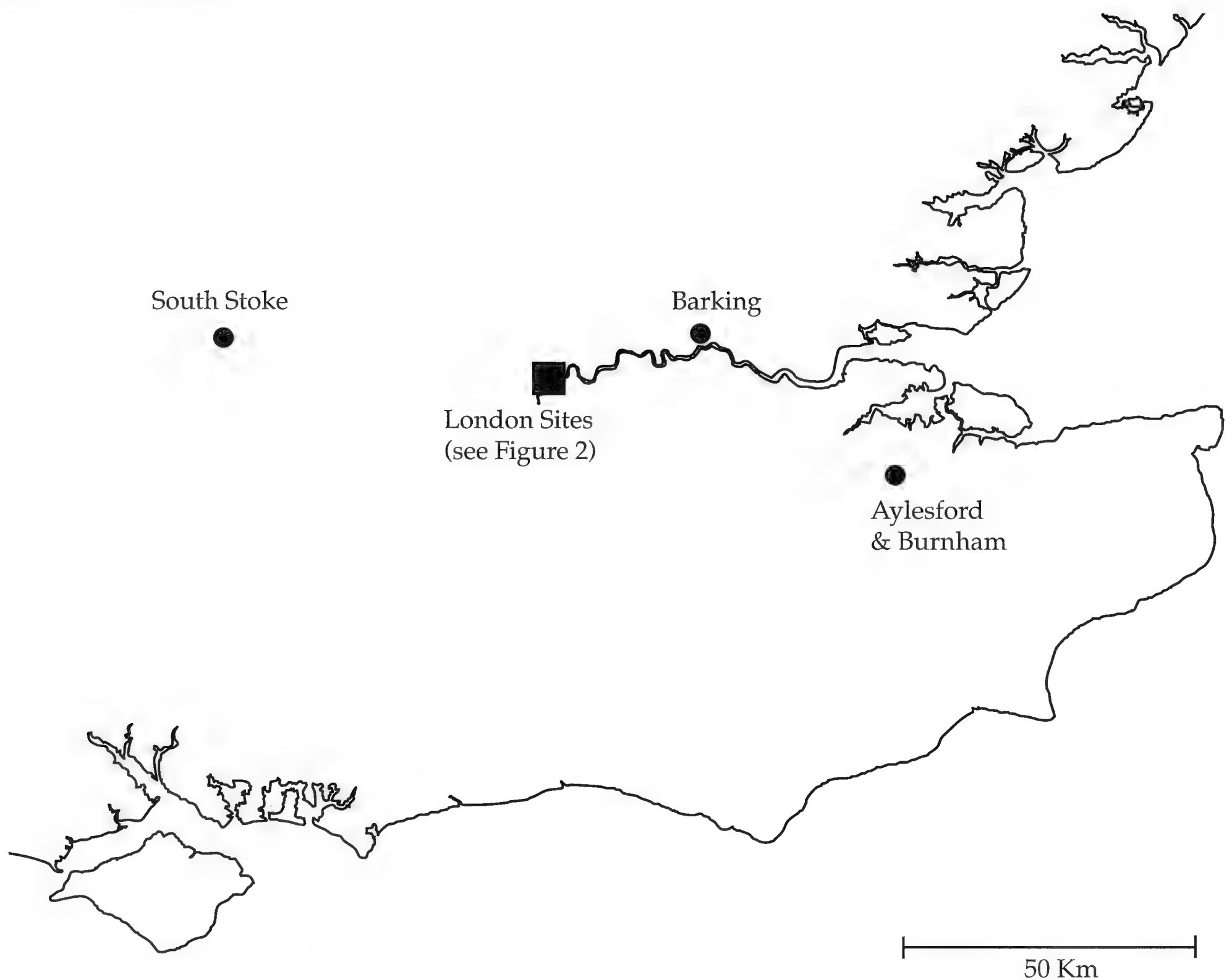
Figure 1   Distribution of *Perforatella rubiginosa* in England

relatively recent colonist in this country.

Perforatella rubiginosa is a mainly eastern European species which extends east into Siberia and west into the main river valleys in Germany, Holland and Belgium (Kerney, Cameron & Jungbluth 1983). It is widespread in Hungary, Poland and Czechoslovakia where it is an inhabitant of the flood zones of rivers (Obrdlik, Falkner & Castella 1995), particularly the freshwater stretches where there is a significant tidal effect. It lives on mud under flood debris usually in areas with sparse tall herbs or shaded by willows and where there is frequent submersion.

In 1995 English Nature funded a survey to obtain up-to-date information on the status of *P. rubiginosa* in Britain. The principal objectives were to assess the status of the snail at each of its known localities, to survey other potential sites, to identify the snail's habitat requirements, and to make recommendations for conservation, management and prospects for a species recovery programme. This paper provides a shortened summary of this work which was first produced as a report to English Nature (Killeen 1995).

METHODS

All known sites for the species were sampled in the river flood zones and the adjacent environment. In addition to the known populations, new sites were sought by selecting potential areas from large-scale maps of the Thames, its estuary and associated river systems. Only sites likely to be suitable for *Perforatella rubiginosa* were surveyed and
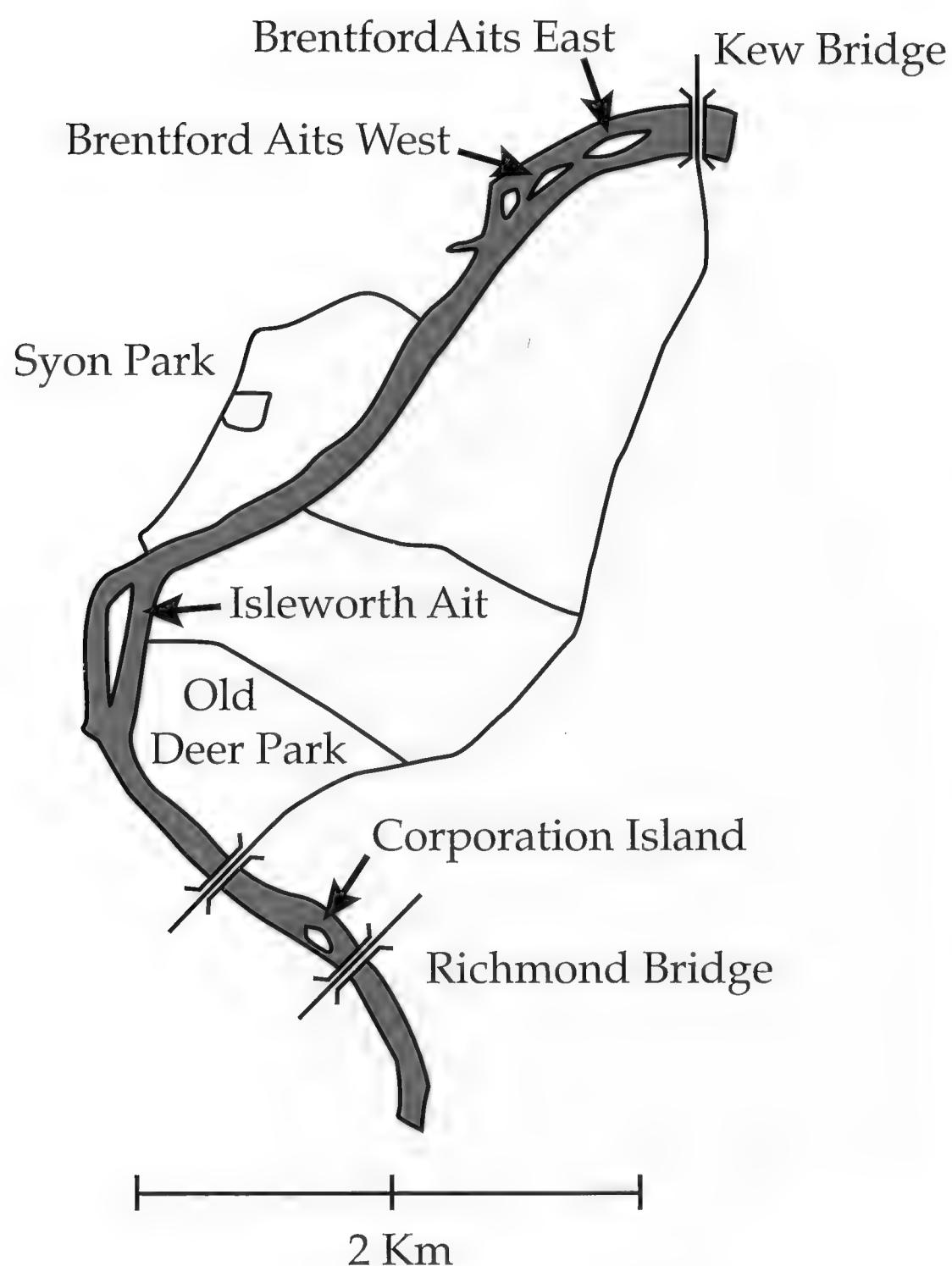
Figure 2   Location of west London sites

therefore all fieldwork was focused on the flood zones of the Thames, Roding and Medway. All of the main survey work was carried out in a six week period during late winter 1995.

Snails were sought in the field by turning logs, bricks and flood rubbish such as plastic bags, reed stems etc. Samples of snails from most sites were collected for morphometric analysis. In an attempt to obtain quantitative data, samples of flood debris were collected from a 0.5m x 0.5m quadrat. This usually resulted in a quantity of litter equivalent to *c*.5 litres. The samples were subsequently dried and the snails picked and counted. However, due to the relatively low density at which *Perforatella rubiginosa* was living, debris sampling was only carried out at 3 locations (Table 3). Numbers of individuals under large items of flotsam were also counted.

The locations of the sites surveyed are marked on the maps Figures 1 & 2.

RESULTS AND DESCRIPTIONS FOR ALL SITES AT WHICH *PERFO-RATELLA RUBIGINOSA* WAS FOUND LIVING

Of the 18 sites examined during the survey, 10 were found to be supporting *Perforatella rubiginosa*:

1. South Stoke, Oxfordshire: River Thames – North Stoke NGR SU607861 to Goring SU601825.
The site studied by Naggs (1982, 1983) and Leighton-Goodall (1996) lies on the east bank of the river between South Stoke ferry and the railway (*c*.1 km of riverbank). The river-bank itself is generally sheer but in places it is 'terraced' and has a tall herb community with sedges (*Carex* spp.), reed canary grass (*Phalaris arundinacea*), willowherbs (*Epilobium* spp.), alder etc. This is backed by a strip of wet grassland (up to 100 m wide) with small patches of *Juncus* and areas of standing water in runnels which may represent old cart tracks or plough lines. There was evidence that the area was grazed by cattle and may also be periodically mowed. A fen with *Carex* spp. and a diversity of wetland flora lies to the east of the meadow.

Much survey time was taken in establishing the precise habitat/zone in which *Perforatella* was living. It was expected that the snails would be living in the tall herb flood zone along the terraces of the riverbank. However, only *Trichia hispida* could be
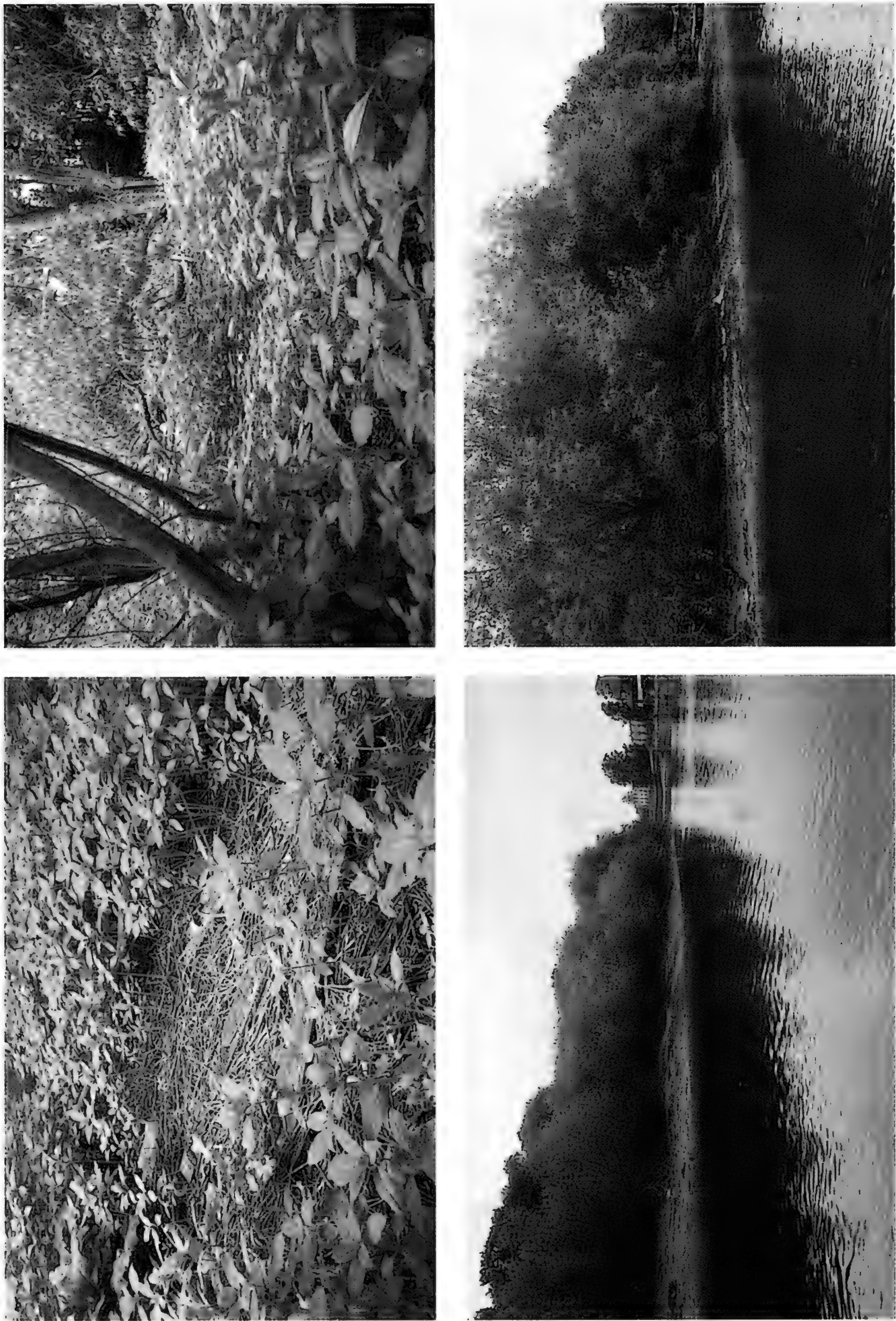
Figure 3 Isleworth Ait, River Thames. 3a - Detail of *Perforatella rubiginosa* habitat with flood rubbish (dead stems and large plank of wood). 3b Floodzone habitat with *Impatiens glandulifera*. 3c - North coast of the island. 3d - North coast of the island (detail).

found there. *Perforatella* was living in the runnels that ran along the meadow/fen margin and where there was a narrow line of flood debris. Specimens were found in an almost submerged environment. A similar habitat with *Perforatella* was subsequently found at several places for a further kilometre to the south of the ferry. A few specimens of *Perforatella* were also found by a riverside fen to the south of North Stoke church.

2. Isleworth Ait: River Thames NGR TQ167759 Figure 3a–d.

This island with a length of *c.*500m and an area of 3.3 hectares lies in the Thames at Isleworth (Figure 2). The east banks past which most of the river flows are relatively steep and in places are piled. The more sheltered west side has more gently sloping banks and a number of small boatyards. The main vegetation type on the island is broad-leaved woodland composed of mainly sycamore, poplar and willow. At the northern end of the island there is a small area of willow/osier carr from where *Perforatella* was first recorded at this site in 1983 and subsequently studied by Mordan & Naggs (1993) and Leighton-Goodall (1996). Work for the present survey was also focused in this area with a more general search made elsewhere on the island.

The main survey area was low lying with large willows and small planted osiers, backed by a bank with a woodland path on top. This maintains the area as a separate habitat. The ground flora at the time of survey was sparse, comprising mainly nettles (*Urtica dioica*) and umbellifers (*Oenanthe aquatica* and *O. crocata*) with some *Rumex* spp. In summer there would be extensive beds of Himalayan balsam *Impatiens glandulifera* (Figure 3b). The area is intersected by muddy rills which in some places penetrate into the main woodland. The habitat is characterized by large quantities of flood rubbish (logs, planks, dead stems, plastic etc) (Figure 3a). A film of surface mud was present over much of the open ground and debris.

Perforatella was very common throughout the survey area and even into the woodland as far as the limit of flood. The largest concentrations were found under planks and plastic sacks (Table 4). A few specimens of *Perforatella* were also found under rubbish in muddy rills along the west bank. [Note - Isleworth Ait is a stronghold for another Red Data Book snail, *Balea biplicata*. Specimens of this species were found abundantly in the main woodland during this survey.]

3. Old Deer Park, Richmond, Surrey: River Thames NGR TQ171751 to 168755

The banks of the river from Richmond Lock to Kew Gardens (and beyond) are made up of steeply angled concrete blocks. However, the towpath is backed by a stream, alder woodland and scrub, marshland etc. Some floodwater from the Thames comes in through culverts. At the time of this survey much of the area was flooded and there were several accumulations of flood debris.

Three specimens of *Perforatella* were found on logs; 2 just north of Richmond Lock and one opposite Isleworth Ait. The latter was under a pile of rubbish above the main river.

4. Brentford Ait West: River Thames NGR TQ184777

Perforatella was recorded as frequent amongst drift debris at the north-east end of the Ait by Adrian Rundle (pers. comm.) in 1983. There is no record of it having been seen since. The island is *c.*300 m long with a vertically piled south bank and a gently sloping north bank. The proximity of Lotts Ait and old boatyards gives rise to a very sheltered environment on the north side. The vegetation is composed of large willows and fallen trunks with a ground flora of mainly small umbellifers (cf. *Oenanthe crocata*) with occasional *Rumex, Urtica* etc. Large piles of flood rubbish (logs, polystyrene, plastic, dead stems etc) had accumulated around trees over most of the island. The open surfaces were covered in a muddy layer of dead leaves.

Perforatella was common below the larger items of flotsam (Table 4) and occasionally

amongst the stem debris.

5. Brentford Ait East: River Thames NGR TQ186778

Although the larger of the 2 islands (*c*.500m long), Brentford Ait East is otherwise very similar to the west Ait. It is piled along the whole length of the south bank whereas the north bank is sheltered and gently sloping. It is covered by large willows and a sparse ground flora: small umbellifers (cf. *Oenanthe crocata*), *Rumex* spp. and *Urtica dioica*. The surface is covered by a layer of muddy leaves and with large accumulations of flood rubbish.

There were no previous records of *Perforatella* from this island, but during this survey it was found to be locally common under larger items of flotsam.

6. Syon Park, Brentford, Middlesex: River Thames NGR TQ173763 to 178770

Perforatella was first recognized in Britain based on specimens collected from Syon Park by Bernard Verdcourt in June 1982 (Verdcourt 1982). The park is bounded by a *c*.1.3km long stretch of the north bank of the River Thames. The site comprises extensive tidal water meadows that are used for cattle grazing. In places there are patches of tall fen dominated by *Glyceria maxima*. The riverbank is characterized by a series of *c*.50 small muddy, tidal rills. A belt of mature willow trees with some poplar extends along virtually the whole length of the bank. Amongst the wooded area there were many fallen trunks in addition to large quantities of flood rubbish (plastic sacks, planks and dead stems). In places the bare ground was covered with a thin layer of muddy leaves. The ground flora in the wooded area was sparse at the time of survey comprising mainly small umbellifers (cf. *Oenanthe crocata*) but in summer it would be dominated by *Impatiens glandulifera*. The search area for this survey was focused on the eastern part of the river bank (an approximately 700m stretch).

Perforatella was locally abundant throughout the woodland area mainly under the logs and planks (Table 4). The zone was well defined and there was no evidence of it in the fen.

7. Corporation Island, Richmond: River Thames NGR TQ176746

Lying between Richmond and Twickenham Bridges, Corporation Island with a length of *c*.140m is the smallest of the Aits surveyed. *Perforatella* was first recorded here in 1983 amongst twig litter under trees. Although the banks are moderately steep and reinforced in places, the island is low lying and probably covered on most high tides. The island is colonized by large willow trees and some scrub, the surface is flat and muddy with a ground flora of mainly small umbellifers (cf. *Oenanthe crocata*) with occasional *Rumex* spp. and *Urtica dioica*. Piles of flood rubbish (mainly dead stems) have accumulated around the trunks of the larger trees. A muddy layer of willow leaves was present over much of the island.

Perforatella was locally distributed over much of the island but was common only under large items of flotsam such as pieces of plywood around the large trees.

8. Barking, Essex: River Roding NGR TQ436844 to TQ436856

Perforatella rubiginosa was first discovered at this site in 1994 by Adrian Norris (Leeds Museum). The survey formed part of an Environmental Impact Assessment on a proposed new R. Roding barrage by the Environmental Consultancy University of Sheffield. The snails were described as "common on mud and debris on the second alleviation lagoon at TQ436847" (Norris pers. comm.). The site lies in a fully urban setting with the river running adjacent to the east side of the A406 North Circular Road. Much of the east bank and parts of the west bank are developed. Piling exists along most of the east bank; the banks of the first and second alleviation lagoons on the west bank have recently been piled.

The first alleviation lagoon (TQ435845) comprises mud with small stands of *Phragmites australis* and is probably submerged on every high tide. The semi-marine prosobranch *Assiminea grayana* Fleming, 1828 was the only mollusc seen. The second alleviation lagoon (the original site) is a series of small 'islands' with a network of channels. They are vegetated mainly by *Phragmites* with other tall herbs: *Urtica dioica*, *Oenanthe aquatica* and occasional *Rumex* spp.; *Ranunculus ficaria* was common on the landward side. The islands are covered by large quantities of flood rubbish: dead stems, logs, planks, plastic bags, and building rubble along the new piling. A similar floodzone habitat with a tall herb community exists on the west bank for a further 0.5km north of the railway. The zone varies in width from 1 to 20m. This then changes at the third alleviation lagoon into a marsh dominated by *Phalaris arundinacea*.

Perforatella was very common on the mud below, and attached to, rubble and larger items of flotsam. Several specimens were also found in a short stretch of floodzone on the east bank.

9. Aylesford, Kent: River Medway – TQ729589 to TQ743583

The population of *Perforatella* at Aylesford was first recognised in January 1983 by Eric Philp. The original site lies on the north bank of the River Medway between the 2 bridges in the village centre. The bank profile essentially comprises a steeply sided intertidal zone capped by a muddy terrace *c*.2m wide which is backed by a herb covered slope *c*.1.5m high. The terrace is sparsely vegetated with *Glyceria* and occasional *Phragmites* and *Oenanthe aquatica*; it is probably covered on most high tides. The slope is herb rich with *Urtica, Rumex, Oenanthe aquatica*, and has lots of rubble and a layer of flood rubbish (dead stems, small logs and planks). *Perforatella* was found on the entire height of the slope mainly on mud amongst the base of herbs and under planks (Table 4) and rubble.

A search was made along the north bank of the Medway as far as the M20 motorway. A habitat precisely the same as that in the village centre could not be found. However, occasional specimens of *Perforatella* were found in places where the bank was gently sloping and a herb community had developed.

A further colony of *Perforatella* was located in a fen to the north of the riverbank towpath just upriver from the bridges. The fen is connected to the river by means of a culvert which floods the southern corner of the fen on a regular basis. The bottom corner is muddy and vegetated by a tall herb community (*Urtica, Rumex, Oenanthe aquatica* etc). This gives way to *Glyceria* swamp on the low-lying ground and willowherb on the higher area. *Perforatella* occurred commonly in the southern corner (quantitative sample see Table 3) but was also found occasionally in the *Glyceria* swamp.

10. Burham Marshes, Kent: River Medway (TQ715613 to 713624)

A small population of *Perforatella* was found by Eric Philp in 1989 amongst flood rubbish at the base of the sea wall at TQ715615. It was found only in small numbers (Philp pers. comm.). An extensive area of riverbank was searched during this survey. Much of the bank to the north of Burham Court church is covered by dense *Phragmites* bed and deep piles of dead stems. Areas of mud with herbs were rare and the habitat did not appear suitable for *Perforatella*. The only mollusc seen commonly was *Assiminea grayana*.

To the south of the church the *Phragmites* is less dense and there are patches of scrub, sedge and tall herbs. Piles of flood rubbish (mainly dead stems) were banked on the mud at the base of the sea wall. No living specimens of *P. rubiginosa* were found although several dead shells were seen on the drifts of debris.

ANALYSIS AND QUANTITATIVE RESULTS

To determine the size distribution of the populations, collections of snails made at all of the sites, apart from Brentford Ait East, were measured. These data (based on shell diameter) are given in Table 1:

TABLE 1
Perforatella rubiginosa shell width (mm) measurements

Site	n	x	σn-1	Range
Aylesford (river)	38	6.52	0.73	4.5 – 7.6
Aylesford (fen)	10	6.77	0.87	5.2 – 7.9
Isleworth Ait	61	6.55	0.63	5.0 – 7.8
Brentford Ait West	13	6.80	0.95	4.2 – 7.8
Corporation Island	32	6.27	0.62	5.5 – 7.4
Syon Park	95	6.05	0.60	5.0 – 7.7
R. Roding, Barking	105	6.20	0.65	4.6 – 7.6
South Stoke (north)	23	4.62	0.74	3.5 – 6.6
South Stoke (south)	17	4.61	0.54	3.8 – 5.6

[n = no. of specimens, x = arithmetical mean shell diameter in mm, σn-1 = sample standard deviation]

The lists of molluscs recorded at all of the *Perforatella* sites, plus results of the quantitative sampling are shown in Tables 2–4:

TABLE 2
Lists of other molluscs associated with *Perforatella* at the main sites

Species	1	2	3	4	5	6	7	8
Lymnaea truncatula		x	x	x	x	x	x	x
Lymnaea peregra		x	x	x			x	
Carychium minimum	x	x		x	x	x		
Oxyloma pfeifferi		x	x	x	x	x	x	x
Succinea putris					x	x		x
Cochlicopa lubrica						x		
Discus rotundatus		x		x	x	x	x	x
Vitrea crystallina		x			x	x		x
Aegopinella nitidula						x		
Zonitoides nitidus	x	x	x	x	x	x	x	x
Deroceras laeve	x	x			x	x	x	x
Deroceras reticulatum	x	x	x	x	x	x	x	x
Balea biplicata		x						
Trichia hispida	x	x						x
Cepaea nemoralis								x

1. South Stoke, 2. Isleworth Ait, 3. Brentford Ait West, 4. Brentford Ait East, 5. Syon Park, 6. Corporation Island, 7. Barking, 8. Aylesford. Note - These lists are of species found living in the same habitat as *Perforatella* and do not represent full species lists for a particular site.

TABLE 3
Results of quantitative quadrat sampling.
* Numbers per 0.5 x 0.5m quadrat (numbers in parentheses refer to density/m²)

		Site	
Species	S. Stoke	Isleworth	Aylesford
Lymnaea truncatula		5 (20)	2 (8)
Carychium minimum	2 (8)	2 (8)	3 (12)
Oxyloma pfeifferi		1 (4)	
Discus rotundatus			2 (8)
Vitrea crystallina		1 (4)	2 (8)
Zonitoides nitidus	1 (4)	1 (4)	3 (12)
Perforatella rubiginosa	3 (12)	2 (8)	3 (12)
Trichia hispida	8 (32)		3 (12)

TABLE 4
Numbers of molluscs under individual items of flotsam
*Numbers under each item of flotsam (numbers in parentheses refer to equivalent values /m²)

	Item (numbers of molluscs)*			
Species	A	B	C	D
Lymnaea truncatula	6 (22)	2 (11)	3 (12)	9 (62)
Carychium minimum	1 (4)			
Oxyloma pfeifferi		5 (27)		
Succinea putris				2 (14)
Discus rotundatus				39 (271)
Vitrea crystallina				2 (14)
Aegopinella nitidula				2 (14)
Zonitoides nitidus	2 (7)		3 (12)	1 (7)
Deroceras laeve		1 (5)		2 (14)
Deroceras reticulatum	11 (40)	4 (22)	7 (27)	1 (7)
Perforatella rubiginosa	17 (62)	12 (66)	30 (117)	6 (42)
Trichia hispida				11 (76)

A Isleworth Ait, plastic sack 44 x 62 cm = 0.2728 m² B Brentford Ait West, plank 101 x 18 cm = 0.182 m² C Syon Park, plank 135 x 19cm = 0.2565m² D Aylesford riverbank, plank 60 x 24cm = 0.144m²

DISCUSSION

During this survey *Perforatella rubiginosa* was found living at most of its previously known British sites, which lie along the Thames corridor. At Burham, Kent, only dead shells were found and Quick's (1960) site at Pangbourne has disappeared as a result of habitat modification (Naggs 1983). The populations at South Stoke, Aylesford and Barking were found to be more extensive than previously recognized. In addition it was found on Brentford Ait East which represents a new site for the species. Occasional specimens found on the riverbank by the Old Deer Park, Richmond are probably only adventives flushed out of nearby populations. At most of these sites *P. rubiginosa* would appear to be thriving. At the larger sites - Isleworth Ait, Syon Park and Barking for example, the populations are large with several hundreds of specimens observed in the field. However, even the other Thames islands, although small in area, support flour-

ishing colonies of *Perforatella*. The results of the quantitative quadrat sampling show that the actual density of snails on the ground is relatively low with values ranging from 8 to 12 individuals per m² (Table 3). However, the equivalent density of snails under large, individual items of flotsam can be as high as 117/m² (Table 4).

Apart from South Stoke, all of the other sites are remarkably similar, lying in the flood-zone of tidal freshwater rivers. They are characterized by having areas of bare mud vegetated by a sparse community of tall herbs particularly *Oenanthe crocata, O. aquatica, Urtica dioica* and *Rumex* spp. In the London sites these communities are within stands of mature willows. Flood rubbish such as planks, logs, dead stems and plastic is a feature at all sites and provides the main refuge for *Perforatella*. Most sites are relatively sheltered and would be gently lapped by a significant proportion of high tides.

The ecology of the South Stoke populations is rather different from those elsewhere. Here *Perforatella* is living in small runnels with standing water in open grassland at the edge of a sedge fen. There is little shading from tall herbs and no trees. Apart from being wet and muddy there are few other similarities. There was only a small drift-line of flood debris rather than the large accumulations found at the other sites. This would suggest that the snails live in an environment that gets flooded on a much less regular basis than those downstream. A further difference in the South Stoke specimens is that they are rarely encrusted with mud, unlike at the other sites where the snails are invariably encrusted (see Figures 4a & d).

The habitat occupied by *Perforatella* is generally unfavourable to many other mollusc species. The associated species at each site are summarized in Table 2. It is only the aquatic *Lymnaea* species, the obligatory hygrophiles *Carychium minimum, Oxyloma pfeifferi, Zonitoides nitidus, Deroceras laeve,* and the ubiquitous *Deroceras reticulatum* that coexist with *Perforatella. Perforatella* frequently occurs on its own or just with the amphibious freshwater species *Lymnaea truncatula* (Table 2). The freshwater amphipod *Orchestia cavimana* Heller, 1865 occurred under flood debris at all of the London and the Barking sites.

The short timescale (late winter) within which this survey was carried out means that a direct comparison of the numerical and size data for the British populations is especially relevant. This reveals that the data for the South Stoke populations fall into a different size class from all of the others. The South Stoke animals have a mean shell diameter of 4.2mm compared to 6.45mm (mean range 6.0 – 6.8mm) for the rest. Apart from South Stoke, the other populations are remarkably similar both in the range of shell size and the mean. It is assumed that this represents a structure ranging from sub-adult to fully-grown adult. Dissection of a few of the larger specimens confirmed that sexually mature adults were present in the populations.

The life history and reproductive cycle of British populations have been studied by Verdcourt (1982), Naggs (1983) and Mordan & Naggs (1993) and Leighton-Goodall (1996). Verdcourt concluded that Syon Park specimens mature in June and over-winter as juveniles with a shell diameter of 5–6mm. Naggs demonstrated that the South Stoke population was reproductively out-of-phase with populations elsewhere. He found that the South Stoke snails over-wintered as full-grown specimens in which the reproductive organs were not completely formed. Sexual maturity was reached in late February and early March. However, research on the South Stoke population by Leighton-Goodall (1996) showed that the snails had not reached adult size in winter, an observation which is supported by the results of the present survey. These results also indicate that *Perforatella* may already be mature by mid-January at the London, Kent and Essex sites.

A limited amount of searching for other sites for *Perforatella* was generally unproductive. In the London area this was less surprising as the species' required habitat is rare and restricted. Of all the sites examined the Surrey bank of the Thames north of Teddington Weir was the most promising. Several places within the tidal zone with the
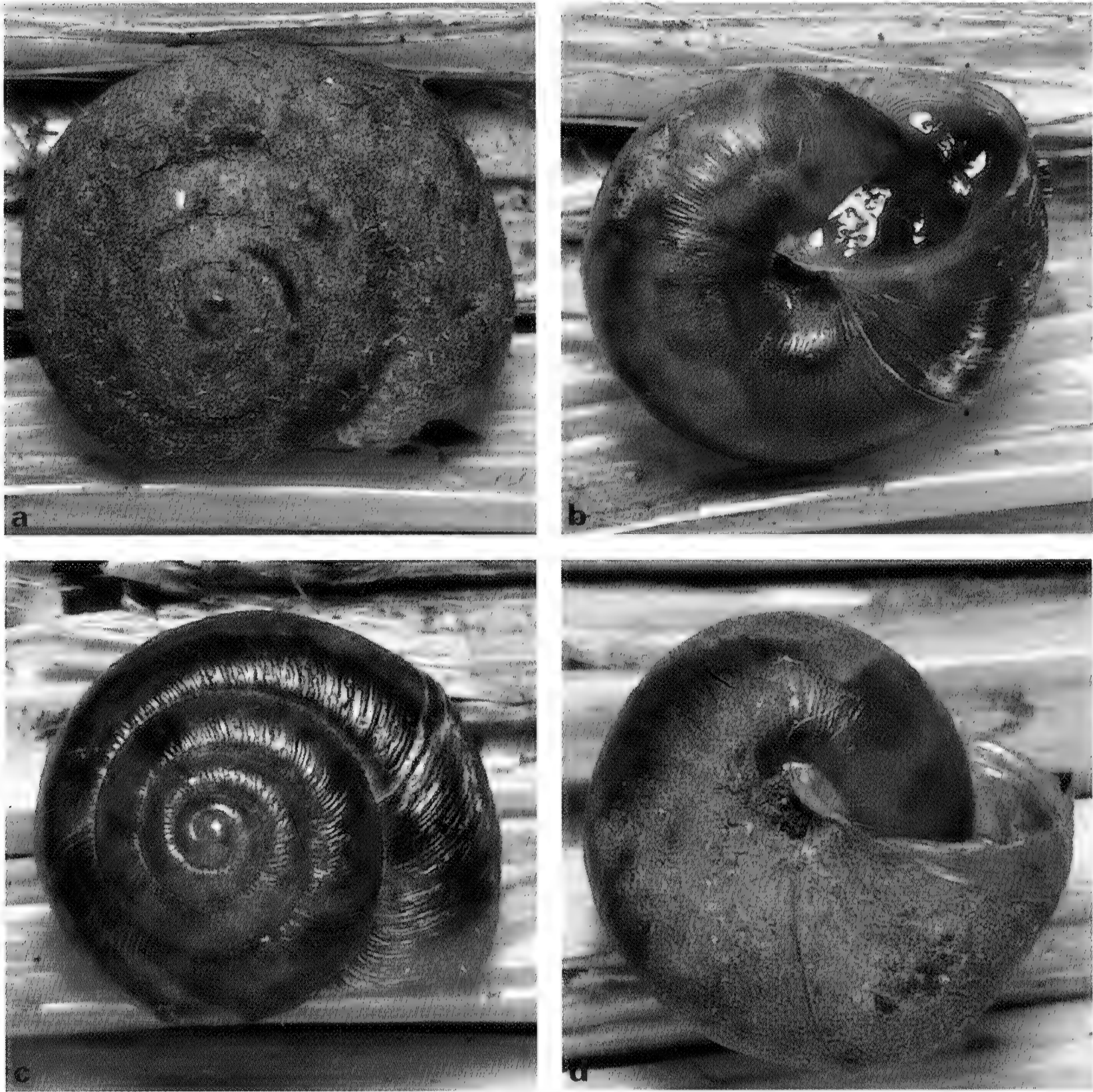
Figure 4a-d   Living specimen of *Perforatella rubiginosa* from Isleworth Ait, River Thames (Actual shell diameter 6.2mm).

right vegetation were found but *Perforatella* was absent. The most likely reason is that none of these sites is as sheltered as those where the snail does occur. There is less protection and therefore flooding would increase the likelihood of scouring of the potential habitat. The Thames above Teddington is not tidal and therefore the specific habitats do not exist. Also, much of the riverside is developed for recreation, housing and parkland. The area around Runneymede appeared to fulfil many of the required criteria. It is curious that the population in Oxfordshire appears to be so restricted. *Perforatella* could not be found elsewhere during this survey and has not been found by the county mollusc recording team.

Although the distribution of *Perforatella* is restricted by availability of suitable habitat, it is unlikely that the few known sites represent the entire British population. Much of the Thames estuary is highly urbanized and industrialized but it is unlikely that the Roding and Medway colonies are the only others outside of London.

Details on the biology and ecology of *Perforatella* elsewhere in Europe are rather scant. The most detailed study is that by Vader (1977) on its occurrence in the Scheldt estuary in Belgium. The Belgian populations show a great number of similarities with those in Britain. Vader records a habitat within the freshwater tidal zone, *Perforatella* occurred commonly on mud and amongst debris in a community of tall herbs dominated by *Urtica* above *Phragmites* beds and shaded by willows. Although it could be found in very high densities, it was restricted in distribution and completely absent from the slopes

above the reach of the tide. Flood rubbish comprising mainly dead reed stems was present as was the freshwater amphipod *Orchestia cavamana*. Vader also records that in eastern Europe *Perforatella rubiginosa* has a much less restricted biotope occurring in all suitable wet habitats even those with a constant water level (see also Obrdlik *et al* 1995).

TAXONOMY

Although a detailed discussion on the taxonomy within the Hygromininae (including *Trichia* and *Perforatella*) is beyond the scope of this paper, it is evident from South Stoke that there are populations whose taxonomic status is unclear. The differences in shell morphology and anatomy are relatively small but the use of modern techniques such as molecular and enzyme analysis should help to elucidate the differences.

There is no doubt that the species found at South Stoke, and formerly at Pangbourne, is a *Perforatella*. However, based on observations during this survey, and by Naggs (1982; 1983 & pers. comm.) and Leighton-Goodall (1996), it might be speculated that it is not the same species as that found at the other British sites. Although the anatomy is very similar the animals do not appear to have the same characteristic pinky-lilac tint possessed by other populations (see Figure 4b). The South Stoke specimens are rarely encrusted with mud, unlike at the other sites where the snails are invariably encrusted. The size structure of the South Stoke population suggests a reproductive cycle that differs from the other British populations. It is generally unusual for one population to be reproductively out of phase with all the other populations in a relatively small geographic area. The habitat at the South Stoke site is also different from the others. Until these problems are resolved, the South Stoke population should be regarded as *P. rubiginosa* and conserved accordingly.

CONSERVATION

The conservation of *Perforatella rubiginosa* at its known sites depends largely on preserving the current status quo. The habitat requirements exist at only a very few sites in London and the Thames Estuary. The lack of disturbance at these sites is certainly an important factor and should be recognized when considering any management plans. The threats to the species are:

- Over management, for example, removal of the fallen logs and flood rubbish for aesthetic reasons, or disturbance when controlling invasive species such as balsam *(Impatiens glandulifera)* and sycamore *(Acer pseudoplatanus)* (e.g. at Isleworth Ait).

- Inhibition of the tidal action by barrages or locks (all sites except South Stoke).

- Piling of the river banks (all sites except South Stoke).

- Development (particularly the Brentford Aits and River Roding). The Aylesford sites are particularly vulnerable and may come under threat from recreational or parkland development.

- Drainage and changes in land use (e.g. South Stoke).

Most of the populations of *Perforatella rubiginosa* are in a state of equilibrium: they

occupy most of the available habitat and are common where they occur. The population size is thus determined by habitat size and the amount of flood rubbish for food and refuge. Whilst the results of this survey have shown that the British populations of *Perforatella rubiginosa* are presently thriving, their restricted habitat and geographical location means they are vulnerable. As such they may merit a higher level of conservation protection than currently afforded, and should at least be subject to regular monitoring surveys by the conservation agencies.

ACKNOWLEDGEMENTS

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SOME QUATERNARY BATHYAL EULIMIDS FROM THE MEDITERRANEAN, WITH DESCRIPTIONS OF TWO NEW SPECIES (GASTROPODA, EULIMIDAE)

I. DI GERONIMO[1] & R. LA PERNA[1]

Abstract   Three bathyal species of the family Eulimidae are reported from the Pleistocene of Southern Italy, Eulima bilineata *Alder, 1848,* Melanella seguenzai *n. sp. and* Campylorhaphion famelicum *(Watson, 1883).* M. seguenzai *n. sp. is markedly close to the Recent Mediterranean* Melanella glypta *Bouchet & Warén, 1986.* Haliella tyrrhena *n. sp., possibly from the Pleistocene as well as from the Holocene, is described from bathyal bottoms in the Tyrrhenian Sea. It is notably close to* H. canarica *Bouchet & Warén, 1986 from the Canary Islands. Other incompletely known deep-sea eulimids from the Mediterranean Pleistocene are briefly discussed.*

Key words   Eulimidae, New species, Bathyal, Quaternary, Mediterranean.

INTRODUCTION

Like most benthic groups, the eulimid fauna from the deep Mediterranean waters is notably poor, compared with the Northeast Atlantic one. Bouchet & Warén (1986) reported 15 deep-sea eulimids from the Mediterranean (18% of the deep-sea eulimids known from the Northeast Atlantic), but very few of them are exclusively known from bathyal depths. However, the deep Mediterranean eulimid fauna may prove to be richer than so far known. A major problem is due to the low density of the deep Mediterranean benthos and eulimids are probably even more scattered and difficult to collect, owing to their specialised parasitic habits on echinoderms (Warén, 1984a; 1990). The deep-sea fossil eulimids (and not only the deep-sea ones) from the Mediterranean are very poorly known. In particular, the Pleistocene deep-sea eulimid fauna can be expected to be more diversified than the Recent one, as is generally known for most benthic groups (see Di Geronimo & La Perna, 1997; Di Geronimo *et al.*, 1997; Di Geronimo *et al.*, in press).

The present work is within a current research on the Plio-Quaternary bathyal molluscs from the Mediterranean. It does not give a complete view of the Quaternary bathyal eulimids, but it would form a starting point to further studies on the composition and the Late Tertiary-Quaternary evolution of this group in the area. Systematics and descriptive terminology are based on Warén (1984a) and Bouchet & Warén (1986).

SYSTEMATIC DESCRIPTIONS

EULIMIDAE
Genus *Eulima* Risso, 1826
Type species *Strombiformis glabra* Da Costa, 1778
Eulima bilineata Alder, 1848
Figs 1-3

Eulima bilineata Alder, 1848: 141.
Eulima bilineata Bouchet & Warén, 1986: 320, figs 754-756.

[1] Dipartimento di Scienze Geologiche, Sezione di Oceanologia e Paleoecologia, Università di Catania, Corso Italia 55, 95129 Catania, Italy.

Material examined   34 shs, Grammichele (southeastern Sicily), Pleistocene deep circalittoral to upper bathyal marls. 22 shs, Vallone Catrica (Messina Strait, southern Calabria), Pleistocene upper bathyal marls.

Habitat   Shelf to bathyal, in 50-900 m (Bouchet & Warén, 1986). In the Pleistocene beds, it is found within deep circalittoral-epibathyal assemblages.

Geographic and stratigraphic range   Known from northern Norway, Iceland-Faroe Islands south to the Mediterranean (Bouchet & Warén, 1986). This is the first documented record from the Pleistocene and as fossil.

Remarks   The history of *E. bilineata* was discussed in detail by Bouchet & Warén (1986), who also stressed the distinctive features from the shallow-water *E. glabra* (Da Costa, 1778). *E. bilineata* is parasitic on some ophiuroids (Warén, 1984b). It has a conical protoconch consisting of *c.* 3.5 convex whorls.

Genus *Haliella* Monterosato, 1878
Type species *Eulima stenostoma* Jeffreys, 1858
Haliella tyrrhena n. sp.
Figs 4-10

Holotype   1 sh, Museo di Paleontologia dell'Università di Catania, Museum number MPC M9 8.6.1999.

Paratype   1 sh, as holotype.

Type locality   Tyrrhenian Sea, off Eastern Sardinia, st BS78/14, 41°21.00'-41°21.04'N, 10°26.05'-10°25.04'E, 1707-1293 m.

Other material examined   1 sh, southern Tyrrhenian, Aeolian Archipelago, Sea, st Eocumm95/28, 38°20'40"N, 15°15'30"E, 820 m.

Measurements   Holotype 2.27 mm high, 0.66 mm broad; paratype 2.09 x 0.67 mm.

Description   Shell small, slender, conical-cylindrical, glossy, transparent, with blunt apex. Last whorl about half of shell length. Protoconch *c.* 370 µm high and 230 µm broad, a little less than 1.5 whorls, the first one strongly convex. Metamorphic line as a sigmoid scar. Teleoconch whorls slightly convex, with shallow but distinct sutures, numbering up to *c.* 4. Subsutural zone flattish. Aperture rather high, *c.* 0.7 of last whorl height, elliptic-elongate, oblique, with angulate posterior ending; maximum width at midpoint. Parietal callus and inner lip thin. Columella faintly twisted, forming a slightly concave line with parietal wall. Outer lip curved with lower part protruding (frontal view), orthocline, broadly and shallowly sinuated below suture, most projecting part well below midpoint (side view). Surface smooth, except for incremental scars (3 in the holotype).

Derivation of name   *thyrrena* from the Latin *Tyrrhenus*, Tyrrhenian; referring to the geographic range.

Habitat   Bathyal, in 800-1700 m.

Geographic and stratigraphic range   Only known from the Tyrrhenian Sea. Some Atlantic
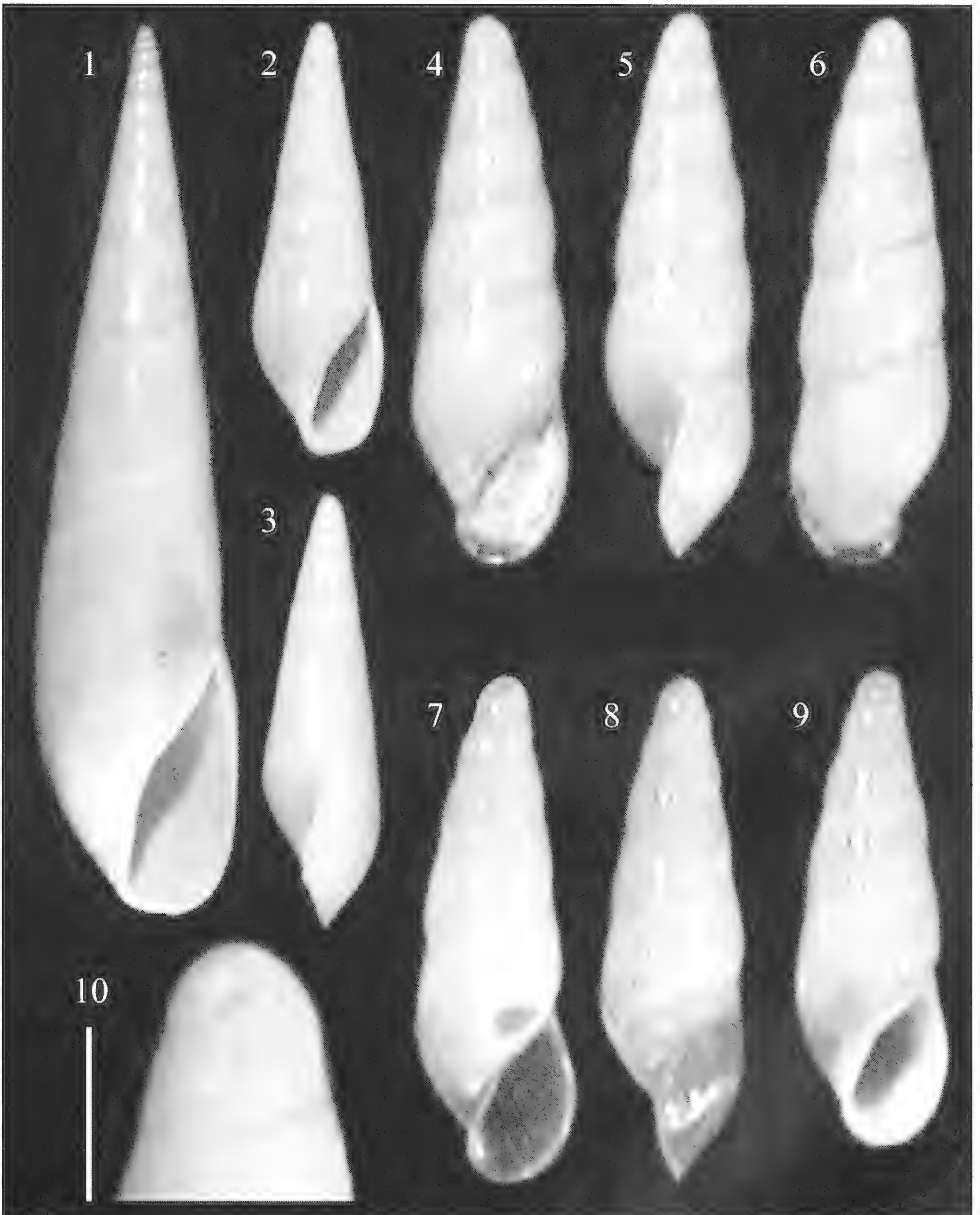
Figs 1-3 *Eulima bilineata* Alder, 1848. **1** Grammichele (9.71 mm). **2, 3** Grammichele (3.60 mm). **Figs 4-10** *Haliella tyrrhena* n. sp. **4-6** Holotype, (2.27 mm). **7, 8** Paratype (2.09 mm). **9** st Eocumm95/28 (1.97 mm). **10** Holotype, protoconch (scale bar = 200 μm).

species, such as *Calliotropis ottoi* (Philippi, 1844), *Capulus simplex* Locard, 1898 and *Scaphander punctostriatus* (Mighels, 1841), were found in the type locality station, thus suggesting a mixture of Late Glacial and Recent thanatocoenoses. The type material is not in fresh condition, but the shell from the Aeolian Archipelago is well preserved and

coming from wholly Holocene assemblages (Di Geronimo *et al.*, in press).

Comparisons   The present species is markedly similar to *Haliella canarica* Bouchet & Warén, 1986, known only from the holotype from the Canary Islands in 590 m. Before remarking the differences, a pen-slip in the original description of *H. canarica* should be pointed out: the shell diameter is not "1.40 mm", but *c.* 0.60 mm, as calculated from the shell drawing and its scale line. The shell shape of *H. tyrrhena* is a little more cylindrical, the teleoconch whorls are more convex and the last whorl is markedly lower. The aperture is narrower, elliptic (rather than pear-shaped) and with maximum diameter at midpoint (rather than close to the lower edge); the inner lip is slightly concave (rather than straight).

Remarks   *H. canarica* and *H. tyrrhena* form a bathyal group distinct from the shelf related *H. stenostoma* (Jeffreys, 1858). Both species have a paucispiral protoconch indicative of non-planktotrophic development, most probably intracapsular, as known for *H. stenostoma* (Bouchet & Warén, 1986: 340). The present-day depth of the Gibraltar sill does not allow non-planktotrophic larvae of deep-sea species to cross (see Bouchet & Taviani, 1992; Di Geronimo *et al.*, in press). This means that the occurrence of the *canarica-tyrrhena* lineage in the Mediterranean must date back to the (Plio)-Pleistocene, when a deeper connection to the Atlantic existed (Roux *et al.*, 1988; Di Geronimo & La Perna, 1997).

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Genus *Melanella* Bowdich, 1822
Type species *Melanella dufresnei* Bowdich, 1822
Melanella seguenzai n. sp.
Figs 11-20

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Holotype   1 sh, Museo di Paleontologia dell'Università di Catania, Museum number MPC M10 8.6.1999.

Paratypes   25 shs (10 partly broken) and 8 fragments, depository and origin as for the holotype.

Type locality   Lazzàro (Messina Strait, southern Calabria), Pleistocene bathyal marls.

Other material examined   22 shs, Archi (Messina Strait, southern Calabria), Pleistocene bathyal marls. 5 shs, Canale (Messina Strait, southern Calabria), Pleistocene bathyal marls. 35 shs, Fiumefreddo di Sicilia (northeastern Sicily), Pleistocene upper bathyal marls.

Measurements   Holotype 3.70 mm high, 1.27 mm broad. Paratypes and other material up to 4.15 mm high.

Description   Shell small, conical, slender, straight to very faintly curved. Apex blunt; spire slightly concave to almost straight. Protoconch somewhat cylindrical, 350-500 µm heigh and 280-340 µm broad, consisting of a little more than 1.5 smooth moderately inflated whorls. Metamorphic line as a slightly sigmoid scar. Teleoconch consisting of up to *c.* 8 whorls (7 in the holotype), moderately convex above suture. Distinct sutures and suprasutural constriction. Last whorl *c.* 0.4 of shell height; periphery narrowly rounded, base convex. Teleoconch microsculpture consisting of dense lines (*c.* 10 per 100 µm), almost straight, reaching from suture to suture, almost lost on base. Incremental scars deeply incised, 0.8-1.3 whorls apart, numbering 7 in the holotype. Aperture *c.* 0.5 of last whorl height, ovate, posteriorly angulate, maximum width at midpoint.
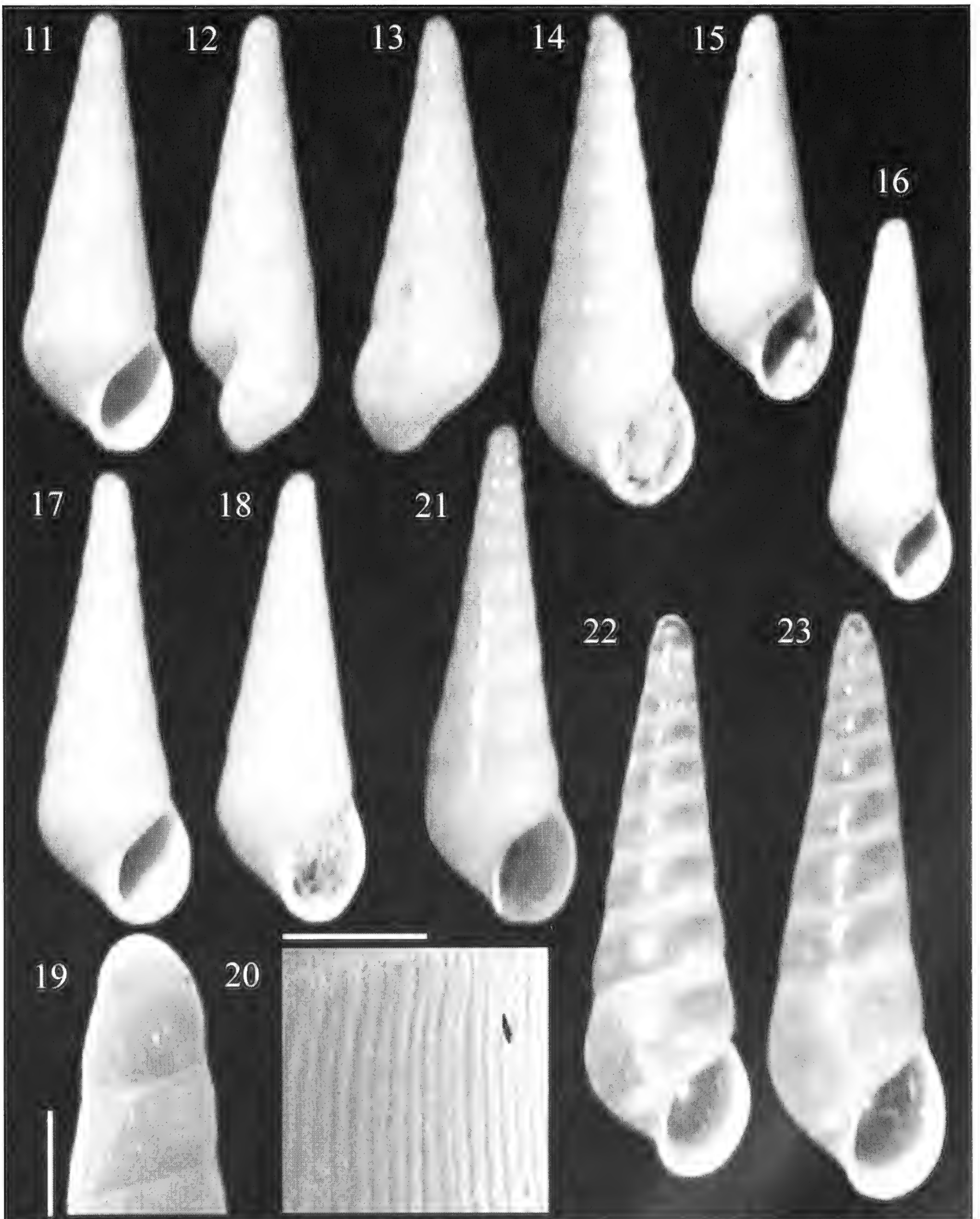
Figs 11-20 *Melanella seguenzai* n. sp. 11-13 Holotype (3.70 mm). 14 Paratype (4.18 mm). 15 Paratype (3.25 mm). 16 Fiumefreddo di Sicilia (3.22 mm). 17 Fiumefreddo di Sicilia, 3.75 mm. 18 Archi (3.75 mm). 19 Paratype, protoconch (scale bar = 200 µm). 20 Paratype, microsculpture (scale bar = 100 µm). Fig. 21 *Melanella glypta* (Bouchet & Warén, 1986), holotype (4.10 mm) (Museo di Zoologia, Bologna). Fig. 22 *Melanella charissa* (Verrill, 1884), Iceland, BIOICE st 2704, 1295 m (4.70 mm) (Icelandic Museum of Natural History). Fig. 23 *Melanella orphanensis* Clarke, 1974, Iceland, BIOICE st 2291, 1206 m, (4.85 mm) (Icelandic Museum of Natural History).

Columellar and parietal callus conspicuous, the former slightly expanded externally. Columella arched. Outer lip curved with lower part slightly protruding (frontal view), orthocline, shallowly sinuated below suture, most projecting part below midpoint (side view).

Derivation of name   Named for the Italian palaeontologist Giuseppe **Seguenza**, pioneer of studies on the Plio-Pleistocene deep-sea faunas from southern Italy.

Habitat   A palaeodepth of 500-600 m is inferred for the type locality beds (Barrier *et al.*, 1996; Di Geronimo & La Perna, 1997). Similar or deeper depths can be inferred for the Archi and Canale beds (Di Geronimo *et al.*, 1997), while the assemblages from Fiumefreddo di Sicilia point to a shallower range (300-500 m).

Stratigraphic and geographic range   Only known from the Pleistocene of southern Italy.

Comparisons   *M. seguenzai* is notably similar to *M. glypta* Bouchet & Warén, 1986, known only from the holotype (Fig. 21), an empty shell from the Sicily Channel in 695-410 m. The differences can be summarised as follows. *M. glypta* has a more slender shell with a distinctly concave outline. Whorls grow more slowly in diameter and height, and the earliest ones are more convex than in *M. seguenzai*. The periphery is well rounded in *M. glypta*, while it appears obscurely angulate in *M. seguenzai*. The aperture is broader and squarish, rather than pyriform-elliptic as in *M. seguenzai*.

The axial microsculpture (Fig. 20) is a remarkable feature of *M. seguenzai* and *M. glypta*. It is similar to that illustrated by Bouchet & Warén (1986, figs 744-746) for the North Atlantic deep-sea eulimid *M. orphanensis* Clarke, 1974. It should be anyway noted that the species reported under this name by Bouchet & Warén (1986), appears notably different from the holotype illustrated by Clarke (1974) (which was not available to the authors). *M. orphanensis* (*sensu* Bouchet & Warén, 1986) (Fig. 23) differs from *M. seguenzai* and *M. glypta* mainly by having a somewhat pointed protoconch (see Bouchet & Warén, 1986, fig. 919) and flatter whorls. The axial lines are less deeply incised, closer (15-30 per 100 μm) and fainter than in *M. seguenzai* and *M. glypta*.

Another deep-sea species from the north Atlantic, *M. charissa* (Verrill, 1884) (Fig. 22), is notably similar to *M. seguenzai* and *M. glypta*. Bouchet & Warén (1986) did not report any microsculpture on this specie, but ill distinct, shallowly incised and straight axial lines are present too. Finally, also *M. densicostata* Bouchet & Warén, 1986 is similar to *M. seguenzai* and *M. glypta*, with a well distinct axial straight riblets 20-30 μm apart.

Remarks   *M. seguenzai* and *M. glypta* form a Quaternary lineage, most probably of North Atlantic affinity. As discussed for *H. tyrrhena*, this lineage is related to Plio-Pleistocene Mediterranean history. However, the single record of *M. glypta* gives no strong evidence about the present-day survival of this lineage in the Mediterranean.

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Genus *Campylorhaphion* Bouchet & Warén, 1986
Type species *Eulima famelica* Watson, 1883
Campylorhaphion famelicum (Watson, 1883)
Figs 24-28, 33

</div>

Eulima famelica Watson, 1883: 121.
Eulima famelica Watson, 1886: 515, pl. 36, fig. 4.
Campylorhaphion famelicum Bouchet & Warén, 1986: 437, figs 924, 1036, 1037, 1040, 1041.

Material examined   1 sh, Grammichele (southeastern Sicily), Pleistocene epibathyal silty
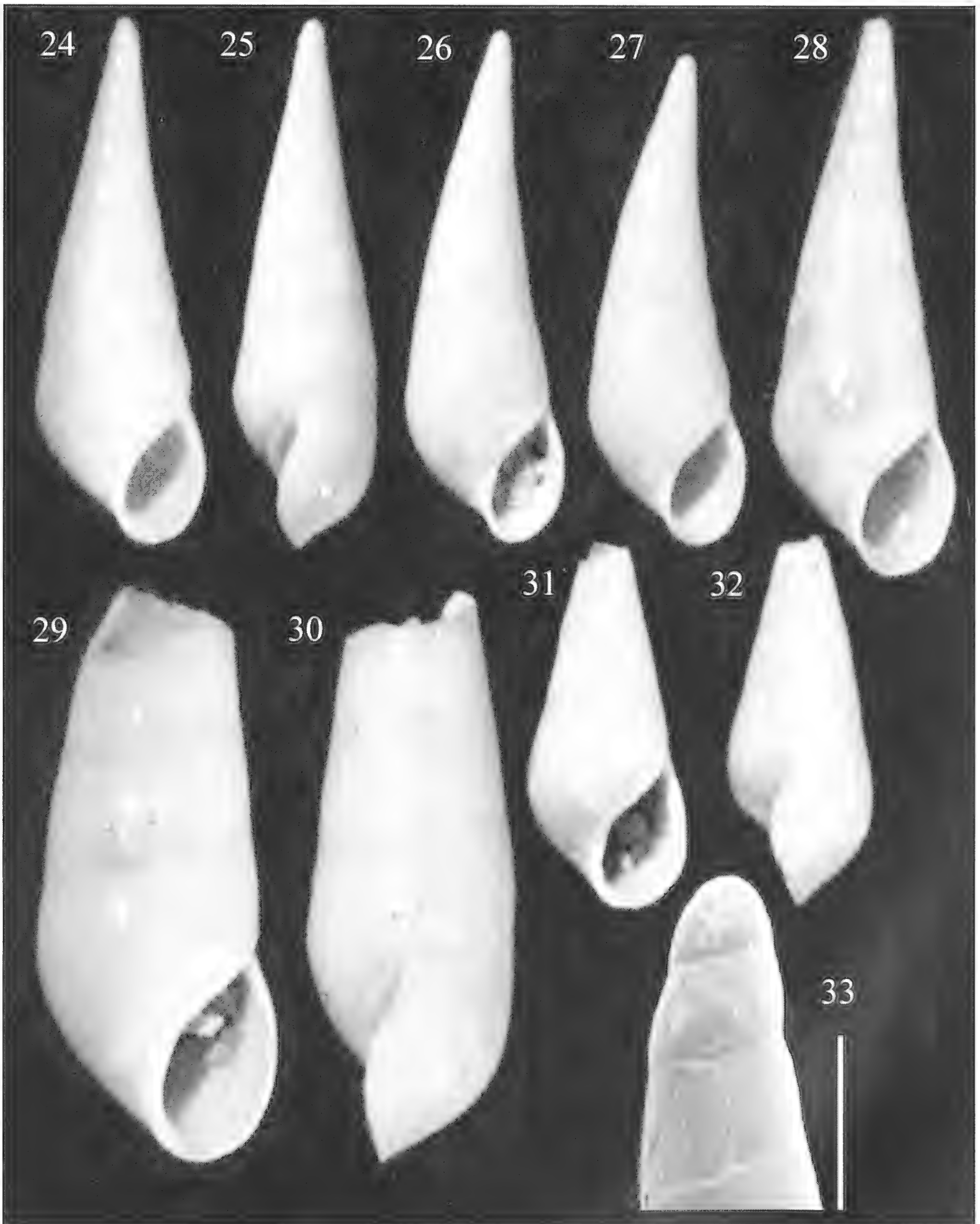
Figs 24-28, 33 *Campylorhaphion famelicum* (Watson, 1883). **24, 25** Bovalino Superiore (4.40 mm). **26** Grammichele (4.30 mm). **27** Archi (4.15 mm). **28** st BS78/14 (4.70 mm). **33** Archi, protoconch (scale bar = 200 μm). **Figs 29-30** *Campylorhaphion* sp., Furnari (4.50 mm). **Figs 31-32** *Fuscapex* sp., Canale (2.95 mm).

marls. 1 sh, Bovalino Superiore (southern Calabria), epibathyal Pleistocene marls. 1 sh, 2 fgs, Archi (Messina Strait, southern Calabria), Pleistocene bathyal marls. 1 sh, off Eastern Sardinia, st BS78/14, 41°21.00'-41°21.04'N, 10°26.05'-10°25.04', 1707-1293 m.

Stratigraphic and geographic range   *C. famelicum* was described from the Azores in 450 fathoms. It ranges from the Bay of Biscay south to the Canary Islands and the Mediterranean (Gulf of Naples), in 190-2000 m (Bouchet & Warén, 1986).

The present record from off Sardinia (Fig. 28) is the second one from the Mediterranean. The shell is in rather poor condition, and may be Late Glacial in age (see under *H. tyrrhena*). The species seems to have been common during the Pleistocene, but its present-day occurrence in the Mediterranean needs to be proved.

Remarks   The protoconch is somewhat cylindrical and consists of *c*. 2.5 whorls (Fig. 33). Bouchet & Warén (1986) remarked a thin sculpture of axial lines for *Campylorhaphion* and described it in some detail on *C. machaeropsis* (Dautzenberg & Fischer, 1896). *C. famelicum* has indistinct straight incised lines, which are not regularly spaced and not always present.

OTHER BATHYAL PLEISTOCENE EULIMIDS

Some fossil species of *"Eulima"* were described by G. Seguenza, mostly from Plio-Pleistocene beds in southern Italy: *E. altavillensis* Seguenza, 1875, *E. conica* Seguenza, 1876, *E. fusiformis* Seguenza, 1876, *E. obtusciuscula* Seguenza, 1876 and *E. polygira* Seguenza, 1876 (see Di Geronimo, 1991). These species were very briefly described and not illustrated. However, only *E. obtusiuscula* can be assumed as a deep-sea species, as its author indicated. It was decribed from Messina as: "Close to *E. glabella* Wood but more slender, with more numerous and more convex whorls". *Eulima glabella* Wood, 1842, a Pliocene species from the Coralline Crag, appears somewhat similar to *M. seguenzai* (Wood, 1848: 98, pl. 19, fig. 2; 1872: 67, pl. 7, figs 4a,b). *Eulima seguenzai* is no more slender, nor has more numerous or more convex whorls than *E. glabella* and therefore cannot be linked with *E. obtusciuscula*. Further, the distinct sculpture of *M. seguenzai* would not have passed unnoticed.

Rindone & Vazzana (1989: 237, fig. 7) reported *Campylorhaphion machaeropsis* (Dautzenberg & Fischer, 1896) from the bathyal beds of Archi, but this record proves to be based on *M. seguenzai*. In the same work, they reported *Ophieulima minima* Dall, 1927 (p. 237, fig. 8). The shell really seems to represent an *Ophieulima*, but the aperture shape appears notably different from that of *O. minima* (see Bouchet & Warén, 1986).

Two shell fragments from the bathyal Pleistocene beds of Furnari (Messina) are referable to *Campylorhaphion*. This material may belong to a distinct species (Figs 29-30), which was misidentified as *Melanella spiridioni* (Dautzenberg & Fischer, 1896) by Di Geronimo & La Perna (1997, tab. 1). It is much larger than *C. famelicum*, and with a comparatively smaller aperture. Finally, two incomplete shells (Figs 31-32) from the Pleistocene bathyal beds of Canale (southern Calabria) may be referred to *Fuscapex* Warén, 1981. Unfortunately, this material is too poor to be described in the present work.

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ASSESSING THE CONSERVATION STATUS OF THE FRESHWATER PEARL MUSSEL IN THE NORTH OF IRELAND - RELEVANCE OF GROWTH AND AGE CHARACTERISTICS

C.R. BEASLEY[1,2] & D. ROBERTS[1]

Abstract In order to conserve the freshwater pearl mussel in Ireland, populations that have a high risk of extinction must be identified and given priority for conservation. Growth of freshwater pearl mussels has been found to vary among populations on a wide geographic scale as well as on a local scale. Populations having a high growth constant (k), because of the small size of individuals and their shorter life-span and thus lower reproductive output, may be more likely to become extinct than those which have a low k and hence larger size and greater reproductive output. This study attempts to estimate the growth constant (k) in rivers in Donegal and Northern Ireland based on measuring the largest shell in each population. Large differences in values of k were found among rivers and these are discussed in relation to catchment bedrock types and the identification of conservation priorities. Appropriate conservation strategies are recommended for Margaritifera margaritifera *populations in the north of Ireland.*

Key words Margaritifera, conservation, growth, age, Ireland.

INTRODUCTION

Because of its long life span (Comfort, 1957), the size and age structure of populations of *Margaritifera margaritifera* are of considerable interest to conservation biologists (Bauer, 1992). One of the most striking features of size and age frequency histograms of many freshwater pearl mussel populations is the lack of mussels smaller than 30 mm and the preponderance of older individuals (Bauer, 1988; Young, 1991).

Growth of freshwater mussels is dependent on temperature (Negus, 1966; Semenova *et al.*, 1992) and slows considerably or ceases completely during the winter (Tevesz and Carter, 1980; Day, 1984). As a result, growth lines are laid down annually in both the shell (Altnöder, 1926) and elastic ligament (Wellmann, 1938) of *M. margaritifera* and other unionaceans (Negus, 1966) and may be used to provide an estimate of the age of individual animals. Construction of age at length curves for freshwater pearl mussel populations has been carried out in various locations (Bauer, 1983, 1986, 1991, 1992; Ross, 1984; Ross, 1988; Semenova *et al.*, 1992; Ziuganov *et al.*, 1994). Investigations by these workers have shown that the growth of freshwater pearl mussels approximates very well to the Von Bertalanffy growth equation (Bertalanffy, 1938), although the parameters determining the equation vary between populations (Bauer, 1991; Ziuganov *et al.*, 1994). The growth constant (*k*) determines the shape of the growth curve, i.e. the rate at which the asymptotic length $L\infty$ is approached. The lower the value of *k*, the slower $L\infty$ is approached and hence growth is slower and maximum size L_{max} is greater (Bauer, 1992; Ziuganov *et al.*, 1994). The maximum age A_{max} is the age at which the asymptotic length is reached and after which no further increase in size occurs with time.

Bauer (1991, 1992) studied the relationship between the maximum observed shell length in a population *(L_{max})* and *k* for a series of populations of *M. margaritifera.* It was found that the interaction between metabolic rate, and hence growth rate, with temperature results in slower growth (low *k*=0.02), larger size and longer life span in the north. By contrast, faster growth (high *k*=0.10), smaller size and shorter life span are characteristics of more southerly populations (Bauer, 1991, 1992). Differences in L_{max} among mussel populations from high and low altitude locations have also been noted (Dyk and

[1] School of Biology and Biochemistry, MBC, The Queen's University of Belfast, Belfast BT9 7BL Northern Ireland.

[2] Current address: Universidade Federal do Pará, Campus de Bragança, Alameda Leandro Ribeiro, S/N, Bragança, CEP 68600-000, Pará, Brazil.

Dyková, 1974). Populations with a small L_{max} have a lower overall reproductive output due to their small size and short life span, whereas populations with a large L_{max} have a greater reproductive output as a result of their long life and large size (Bauer, 1992). The former may be more liable to extinction than the latter especially where water quality is poor and juvenile mortality is high (Bauer, 1991), and where the host fish density is low. Some mussel populations vary in the age at first reproduction (Young and Williams, 1984) and those high k populations that reproduce earlier may compensate for lower reproductive output as a result of their shorter life span. Similarly, a shorter parasitic phase, as has been found for some populations (Bauer, 1979) and perhaps combined with a long breeding episode, may allow more host fish to be infected with glochidia of high k mussel populations. In populations with low k and a long life span, recruitment of juveniles may never occur because of poor interstitial water quality or low host fish density, although adults may persist for decades under such adverse conditions.

Conservation of freshwater pearl mussels therefore depends to some extent on the identification of priority populations through estimation of their growth, length and age characteristics. Besides these, other criteria that need to be taken into account when evaluating conservation priorities of mussel populations are the suitability of the habitat, mussel density, density of host fish and occurrence of pearl fishing. Those populations most at risk of extinction must be among the first to be evaluated as to the chances of success of a conservation programme, taking all the above criteria into account.

The aim of this study is to estimate the growth constant (k) of freshwater pearl mussel populations in the north of Ireland using Bauer's (1992) model and so to assess their conservation status, using growth, length and age characteristics.

METHODS

The majority of mussels measured were those sampled during surveys of *M. margaritifera* in Donegal and Northern Ireland (Beasley & Roberts, 1996; Beasley, Roberts & Mackie, 1998). Mussels were measured to the nearest millimetre along the longest distance from the anterior to the posterior of the shell (L) using Vernier callipers. At each site up to 50 individuals were measured. A size frequency distribution was constructed for each river population combining data from individual sites. The observed maximum length L_{max} was recorded for each river.

The values of L_{max} for all mussel rivers were input into regression formulae from a model of the relationships between L_{max}, k, L_∞ and A_{max} developed by Bauer (1992) from which k, L_∞ and A_{max} were estimated for each population. As the model calculates k on a 5 year basis, the value of k obtained was divided by 5 to give the annual growth constant. Estimates of k were not possible for some rivers as the observed L_{max} values were outside the input range of the model. Bauer's model is based on the von Bertalanffy growth equation to which growth data from several Irish freshwater pearl mussel rivers (Ross, 1984; Ross, 1988), including some being considered here (see Beasley, 1996), have been successfully fitted.

RESULTS

Figure 1 shows that mussels below 30 mm are generally absent from the north of Ireland. Where they do occur, in rivers H, J and N, they are only found in very low numbers (Figure 1). Mussels between 31 and 60 mm were found in low numbers in rivers D, G, I, L and P (Figure 1). Many rivers (A, B, C, E, F, K, M and O) did not contain mussels
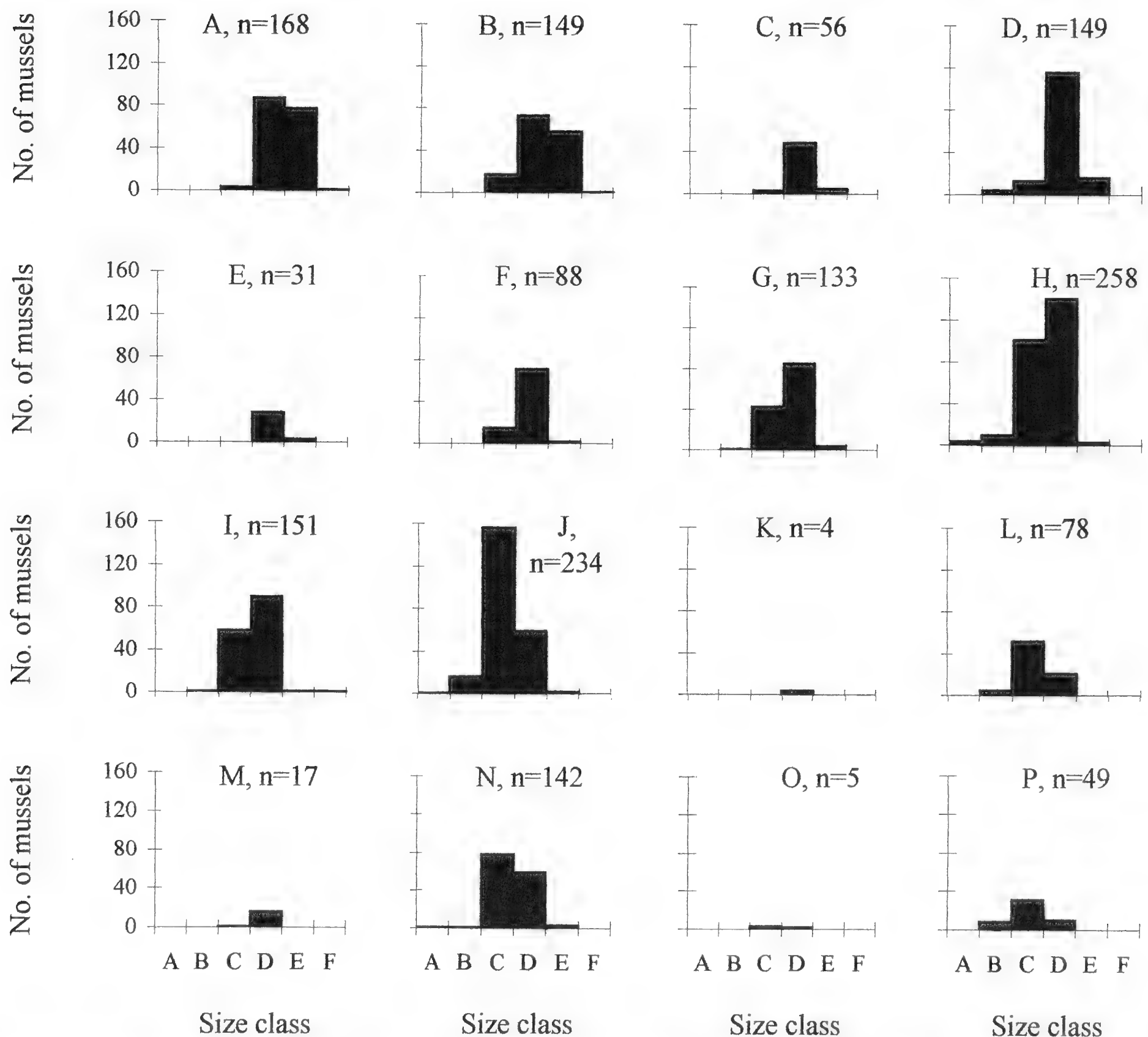
Figure 1 Size frequency distributions of mussels from north of Ireland rivers. Size classes (in mm) are: A: 0-30; B: 31-60; C: 61-90; D: 91-120; E: 121-150 and F: 151+. n refers to the number of mussels measured.

any smaller than 61 mm (Figure 1). Populations with the majority of mussels between 91 and 150 mm in length include rivers A-E (Figure 1). The majority of mussels from the remaining rivers (F-P) are between 61 and 120 mm in length (Figure 1).

Values of k, L_∞ and A_{max} for north of Ireland populations predicted by Bauer's (1992) model are given in Table 1. The predicted value of k ranges between 0.016 for river E and 0.107 in river P. The predicted value of L_∞ varies between 99 mm in river P and 161 mm in river A (Table 1). The predicted maximum age ranges between 55 years in river P and 110 years in river A (Table 1).

The overall ranking of rivers in terms of their growth and age characteristics places rivers A-F as those containing mussels with the largest shell sizes, slowest growth rates and longest life spans (Table 1). These rivers occur on predominantly granite bedrock. Although not estimated for some rivers because L_{max} was outside the range of the model, k values should be low because of the large shell size. Rivers G-K harbour mussels with moderate shell sizes, moderate growth rates and medium life span (Table 1). These rivers occur on limestone or granite and quartz bedrock types. Finally, mussels inhabiting rivers L-P have the shortest shell sizes, fastest growth rates and shortest life spans (Table 1). Rivers L-P occur on either limestone or granite bedrock types.

TABLE 1

Annual growth constant (k), asymptotic length (L∞) and maximum age (A_{max}) of north of Ireland mussel populations predicted by Bauer's (1992) model using L_{max} observed in the field as input. Estimates of k were not calculated for rivers A-D as the observed L_{max} values were outside the input range of the model. The predominant type of bedrock found in each catchment is also given.

Region	River	k	L∞ (mm)	Lmax (mm)	Amax (years)	Bedrock type of catchment
Donegal	A	*	161	152	110	Granite
Donegal	B	*	160	151	109	Granite
Northern Ireland	C	*	147	141	98	Granite
Donegal	D	*	137	133	89	Granite/quartzite
Northern Ireland	E	0.016	131	128	84	Granite
Northern Ireland	F	0.023	129	126	82	Granite
Northern Ireland	G	0.03	126	124	79	Limestone
Donegal	H	0.033	125	123	78	Limestone
Donegal	I	0.037	124	122	77	Granite
Donegal	J	0.040	123	121	76	Quartzite
Northern Ireland	K	0.047	120	119	74	Quartzite
Northern Ireland	L	0.051	119	118	73	Limestone
Northern Ireland	M	0.054	118	117	72	Limestone
Donegal	N	0.058	117	116	71	Granite
Northern Ireland	O	0.075	110	111	65	Limestone
Donegal	P	0.107	99	102	55	Quartzite

DISCUSSION

Growth is very slow in freshwater pearl mussel populations (between 60° N and 30° N) in which k ranges from 0.018 to 0.108 (Bauer, 1992; k value adjusted to annual figure). In constrast marine bivalves such as *Ostrea edulis* in Wales may reach k values between 0.35 and 0.41 (Richardson *et al.*, 1993) and in some European unionids remarkably high k values of up to 1.75 may occur (Bauer *et al.*, 1991). These differences are probably related to the higher temperatures and nutrient status generally found in other habitats, such as unionid rivers (Bauer *et al.*, 1991) or the sea, rather than in *Margaritifera* rivers.

In the present study, remarkable variation in the growth constant occurs among north of Ireland populations (k, 0.016 to 0.107) and is almost equal to the range of k values found by Bauer (1992). Similarly, k is highly variable among freshwater pearl mussel populations in other regions throughout its range (Table 2), for example, Bavaria (k, 0.054 to 0.124) and the West of Ireland (k, 0.067 to 0.147). Although impossible to estimate, the k values for the rivers in which L_{max} exceeded the maximum input value of the model may be very much lower than the smallest k value recorded in the present study. Variation in growth and size (Table 2) is a very plastic trait among freshwater pearl mussels (Bauer, 1991) and is correlated with hydrochemistry (Björk, 1962; Bauer, 1992), latitude (Bauer, 1992) and altitude (Dyk and Dyková, 1974). Thus there is potential for regional variation depending on local conditions. All the rivers with large shells and low k values occur on poorly weathered granite bedrock whereas rivers G, H, L, M and O, which have small shells and high k values, occur on predominantly limestone rocks which are easily weathered. Differences in bedrock types resulting in differences in hydrochemistry may thus influence k. Mussel populations in Rivers N and P have high

k values despite occurring in predominantly non-calcareous bedrock. Lakes feed both of these rivers and the effect of relatively more productive and warmer water flowing from the lake may modify the growth constant.

Different environments impose resource limiting conditions under which characteristic maximum sizes ($L_∞$'s) are attained (Seed, 1980). In several catchments, and particularly in rivers G, L, M and O in the Erne catchment in Northern Ireland, where *M. margaritifera* co-occurred with *Anodonta* sp. and crayfish *Austropotamobius pallipes* (Beasley *et al.*, 1998), the presence of base-rich limestone rocks (Geological Survey of Ireland, 1962) may influence primary productivity and result in an increased k value. These populations appear to have faster growth, smaller maximum size and a shorter life-span than those in rivers A-F, which occur in base-poor granitic areas (Geological Survey of Ireland, 1962). Studies in the north-west of Russia (Semenova *et al.*, 1992) and Bavaria (Bauer, 1991) revealed that growth rates of freshwater pearl mussel populations were greater in areas where the underlying rock was base-rich and easily eroded and lower in areas where acidic and less easily eroded rock occurred (See Table 2).

Maximum age is quite variable among north of Ireland populations (Tables 1 and 2). Wide variation in maximum age among populations was reported by Ross (1984) for the west of Ireland and Mackie (1992) for Northern Ireland (Table 2). Ross (1988) determined the A_{max} of the population from River A in Donegal to be 98 years whereas in the present study a value of 110 years was recorded for the same river. However, the L_{max} observed in both studies was similar (153 and 152 mm respectively).

TABLE 2

Values obtained from the literature of the growth constant k, maximum observed length L_{max} and maximum observed age A_{max} of *M. margaritifera* populations from different parts of its range.

Location	k	Lmax (mm)	Amax (years)	Reference
Latitude 60° Europe & USA	0.018	145	132	Bauer (1992)
Northwest Russia	-	115-125	80+	Semenova *et al.* (1992)
Varzuga R., NW Russia	0.03-0.063	76-110.5	62-99	Ziuganov *et al.* (1994)
Keret R., NW Russia	0.041-0.059	56-162	99-114	Ziuganov *et al.* (1994)
Arctic Sweden	-	145	116	Hendelberg (1961)
Southern Sweden	-	50-110	20	Björk (1962)
West of Ireland	0.067-0.149	112.6-155.9	36+-123+	E. Ross (1984)
North of Ireland	0.016-0.107	102-152	55-110	Present study
Northern Ireland	-	155	22-100+	Mackie (1992)
Donegal	0.041	153	98	Ross (1988)
South of Ireland	-	148	-	Lucey (1993)
Northern British Isles	-	112-150	-	Chesney *et al.* (1993)
Southern British Isles	-	93-110	-	Chesney *et al.* (1993)
Northern Bavaria	-	-	60-110	Bauer (1983)
Vogelsberg, Germany (basalt)	-	42-122	70	Jungbluth & Lehmann (1976
Bavaria (primary rock)	0.054	150	-	Bauer (1991)
Bavaria (sandstone)	0.124	120	-	Bauer (1991)
Northwest Spain	-	-	40-60	Bauer (1986)
Montana, USA	-	100	67	Stober (1972)
Latitude 30° Europe & USA	0.108	80	30	Bauer (1992)

In some populations, such as those in rivers K and O, very low numbers of individuals were observed and it is possible that L_{max} may be biased because of the small sample size. Because k depends on the value of L_{max}, sampling of mussels smaller than the

maximum size that exists in the field may overestimate k and underestimate A_{max} and L_∞. In growth and age determination studies it is therefore necessary to sample the largest individual in the population. Pearl fishermen preferentially remove the largest mussels and therefore sampling in heavily fished rivers may result in an underestimation of L_{max} and so lead to a larger k value. This may also occur where deep and fast flowing water make sampling difficult. Practically all mussel rivers in Donegal and Northern Ireland have reports of being fished in the recent past (Beasley & Roberts, 1996; Beasley et al., 1998) and the k values reported here may be overestimated because of the difficulty in finding the largest shell. However, the effect of pearl fishing on the size frequency distribution of mussels in Irish rivers is not very clear given that, of the rivers with a long and well-documented history of pearl fishing, two (rivers A and B) had the largest shells in this study. River P with the smallest L_{max} has no records, anecdotal or otherwise, of pearl fishing. If fishing effort is similar in all rivers then, although L_{max} and k values may not be true estimates, they may at least be useful in comparisons of rivers from the same region.

In rivers O and P, the L_{max} value was greater than the L_∞ value. It is possible for the observed maximum length to exceed L_∞ due to individual variation within the population (Bauer, 1992). The L_∞ is simply the maximum length the average individual can attain growing under the conditions of the von Bertalanffy curve (Bauer, 1992).

The fact that the growth constant is correlated with maximum age and maximum shell length of mussel populations (Bauer, 1991; 1992) is significant in terms of conservation. Determination of these basic parameters can help in the identification of priority populations since their small size, short life span (high k) and hence low reproductive output make them more susceptible to extinction than their larger, longer-lived counterparts (low k) (Bauer, 1991). Furthermore, measuring L_{max} in situ removes the need to sacrifice large numbers of mussels in each population in order to determine the growth parameters directly from length and age data.

Bauer (1991) suggests that over-age populations with large shells, slow growth and a long individual life span may persist for many decades particularly where the water quality is good. This appears to be the case with several populations (A-F). Mussels from other rivers (G-K) have medium sized shells, medium k values and in some (H and J) there is evidence of recent recruitment (Beasley and Roberts, 1996). Mussels in rivers L-P have smaller maximum lengths, higher growth constants and lower maximum ages than the other populations examined in the present study. According to Bauer (1991), such populations are most vulnerable to the risk of extinction and there is a high risk of population decline where $k>0.1$ and the mortality rate of juveniles in the sediment is high (Bauer, 1991). Only one of these rivers (N) has mussels smaller than 30 mm, although even these are few in numbers.

Regardless of the k value, where mussel numbers are high, water quality is good and host fish present, the best conservation strategy to adopt is the introduction of infected fish and rigorous control of pearl fishing. Since high k populations are more at risk of extinction than low k ones, priority should be given to the former. Where numbers of mussels are small, habitat is unsuitable and host fish in low abundance or absent, the conservation programme should first aim to improve water quality so that infected fish may eventually be introduced. As high k populations may easily go extinct before this long-term goal is reached it may be a better strategy to give priority to low k populations which can persist for many years under sub-optimal conditions.

Chesney et al. (1993) recommended urgent measures to be taken to protect the Nore freshwater mussel in view of its unique association with calcareous waters and their characteristic species. Several Northern Ireland rivers may also harbour a hard-water form of *M. margaritifera* (Beasley et al., 1998) and efforts should be made to ensure that these and other hard water populations in Ireland (Lucey, 1993) are maintained so as to

protect maximum biodiversity. These populations have moderate to high *k* values but only two (G and L) have reasonably large numbers of mussels and therefore should be given immediate conservation priority.

Appropriate conservation measures are to prevent pearl fishing, improve or maintain suitable habitat conditions such as water quality, and enhance mussel and host fish stocks. The latter may be achieved by introducing artificially infected fish (Bauer, 1991) or cultured juveniles (Buddensiek, 1995). Further discussion of these topics for various parts of Europe can be found in Valovirta (1990); Bauer (1991); Young (1991); Wells and Chatfield (1992) and Woodward (1994). Only until pearl fishing is prevented and the habitat is suitable, can attempts to enhance recruitment be initiated and evaluated.

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A REVIEW OF THE STATUS, DISTRIBUTION AND HABITAT REQUIREMENTS OF *VERTIGO MOULINSIANA* IN ENGLAND

C.M. DRAKE[1]

Abstract   Recent recording indicates that Vertigo moulinsiana *is not as rare as previously thought. Records are grouped by river catchment which emphasises a close association with rivers in calcareous or base-rich areas of England; the association with fens is less strong. Its widespread occurrence shows that it is not dependent upon ancient, undisturbed habitats but it does mainly occupy sites with unintensive management, as indicated by over half of the sites with records made since 1970 falling within 43 Sites of Special Scientific Interest. The snail is most often found on large species of* Carex *and* Glyceria maxima, *and less frequently on* Phragmites, Phalaris *and other large plants. England appears to support an important proportion of the European population; in recognition of this, five Special Areas of Conservation have been proposed for it.*

Key words   Vertigo moulinsiana, *distribution, ecology, conservation.*

INTRODUCTION

Vertigo moulinsiana (Dupoy, 1849), sometimes known in the UK as Des Moulins's whorl snail, was until recently little known to most invertebrate ecologists and known only by name to most conchologists. Its inclusion in the European Community (EC) Habitats and Species Directive (92/43/EEC) changed this perspective dramatically and brought the species to the attention of conservation biologists and incidentally to the public when it was found on the route of the Newbury by-pass in southern England (Stebbings & Killeen, 1998).

The Directive places several obligations on member states. These include designating Special Areas of Conservation (SAC) for species listed in Annex II of the Directive, maintaining favourable conservation status for the species across its range and reporting to the EU on actions and results of monitoring its status (Commission of the European Communities, 1992). As a consequence of the snail being listed in the Habitats and Species Directive, it was included in the UK Biodiversity Action Plan (BAP) which gives action plans for 112 species of plants and animals (UK Steering Group, 1996). The published plan for *Vertigo moulinsiana* makes recommendations for action that supports and goes beyond the requirements of the Habitats and Species Directive. Unlike the EC Directive, the UK plan stresses the need for local action, a call that has been heeded enthusiastically by several local authorities and conservation organisations (e.g. Baker & Howlett, 1997).

It is therefore appropriate to make information on distribution more widely available and to bring together recent increases in understanding of the species' ecological requirements to help formulate local action plans and management plans. English Nature commissioned several studies following representation from members of the Conchological Society who reported finding potentially large populations of the snail in the Kennet valley (Drake, 1997). This information was used in helping to select SACs (Drake, 1998) and it is hoped that it will have wider application in taking forward the Biodiversity Action Plan.

[1]English Nature, Northminster House, Peterborough, PE1 1UA.
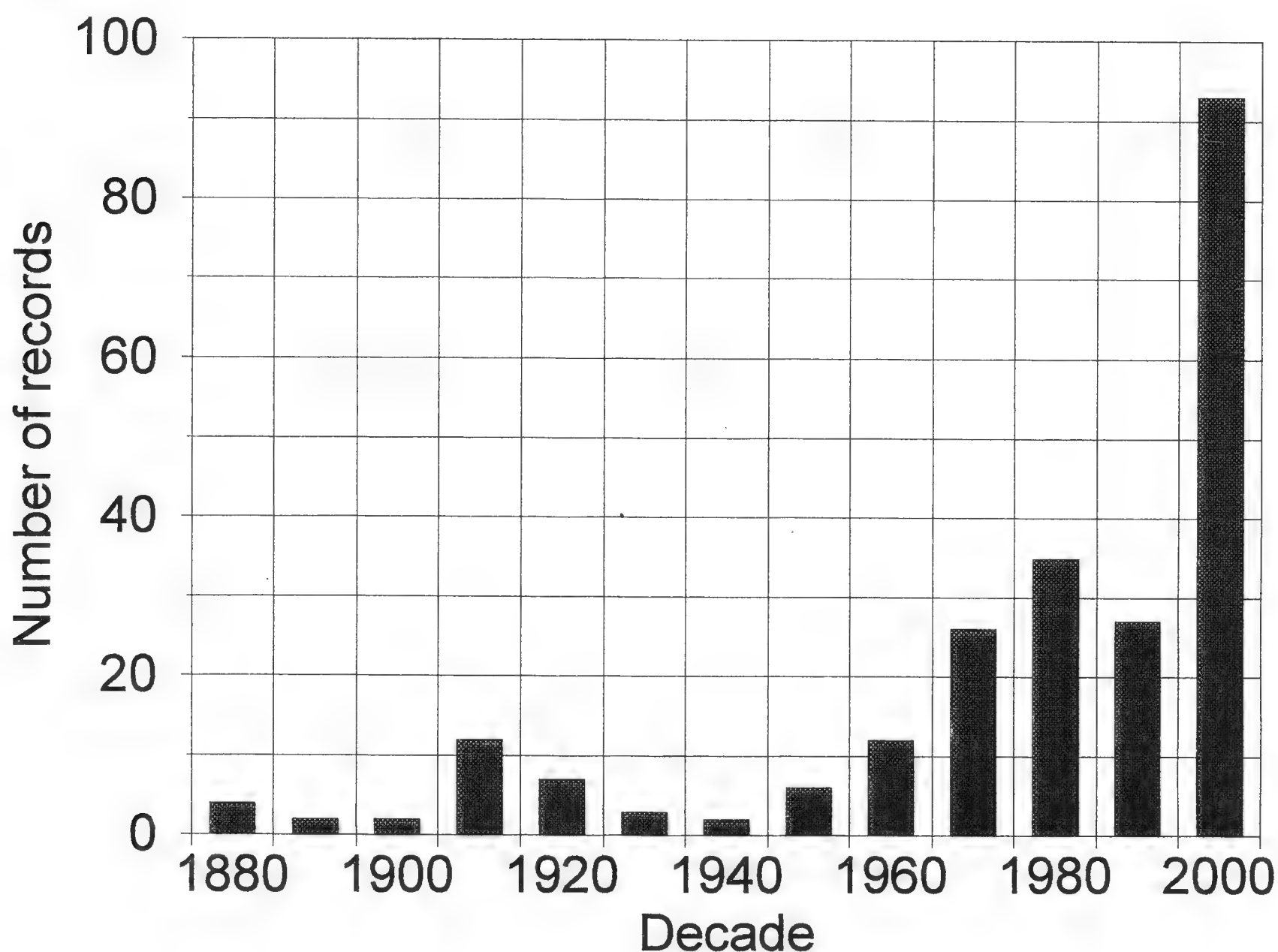
Fig. 1 Number of records per decade.

Methods

Information on the current distribution of *Vertigo moulinsiana* in Britain was obtained mainly from records submitted to the Conchological Society's national recording scheme for terrestrial and freshwater molluscs. Information quoted from these record cards is not referenced in the text. The database was searched in 1996, since when further records have been submitted to the national recorder, not all of which have been used in this paper. These additional records are unlikely to alter the conclusions drawn here. Additional information was obtained from surveys commissioned by English Nature (Chatfield, 1996; Killeen, 1996a, 1996b; Kirby, 1996) and from work undertaken by Willing (1996; pers comm.). Data on the European status of the snail was provided by Seddon (1996) who updated information compiled by Killeen (1996c). The available records have been entered into the Invertebrate Site Register of nationally scarce and rare species maintained by the country conservation agencies (Ball, 1994). Published sources of some records are given but it is not intended that this paper should provide an exhaustive bibliography for this species.

Results

Recording history

Jeffreys (1862) predicted that *V. moulinsiana* would be found in England after he discovered it in Galway, Ireland, in 1845. The first English record was from Hampshire in 1877 (Groves, 1880). Since then, over 240 records of *V. moulinsiana* have been made from 165 localities which can be identified with reasonable confidence to within at least a 1 km square of the National Grid. These represent a small proportion of the records submitted to the recording scheme for terrestrial and freshwater molluscs for which 115,000

Fig 2 Distribution of *Vertigo moulinsiana* by location in the south-east of its range. Each dot is about 5km in diameter. Only larger rivers are shown and only those within the catchments where the species is known.
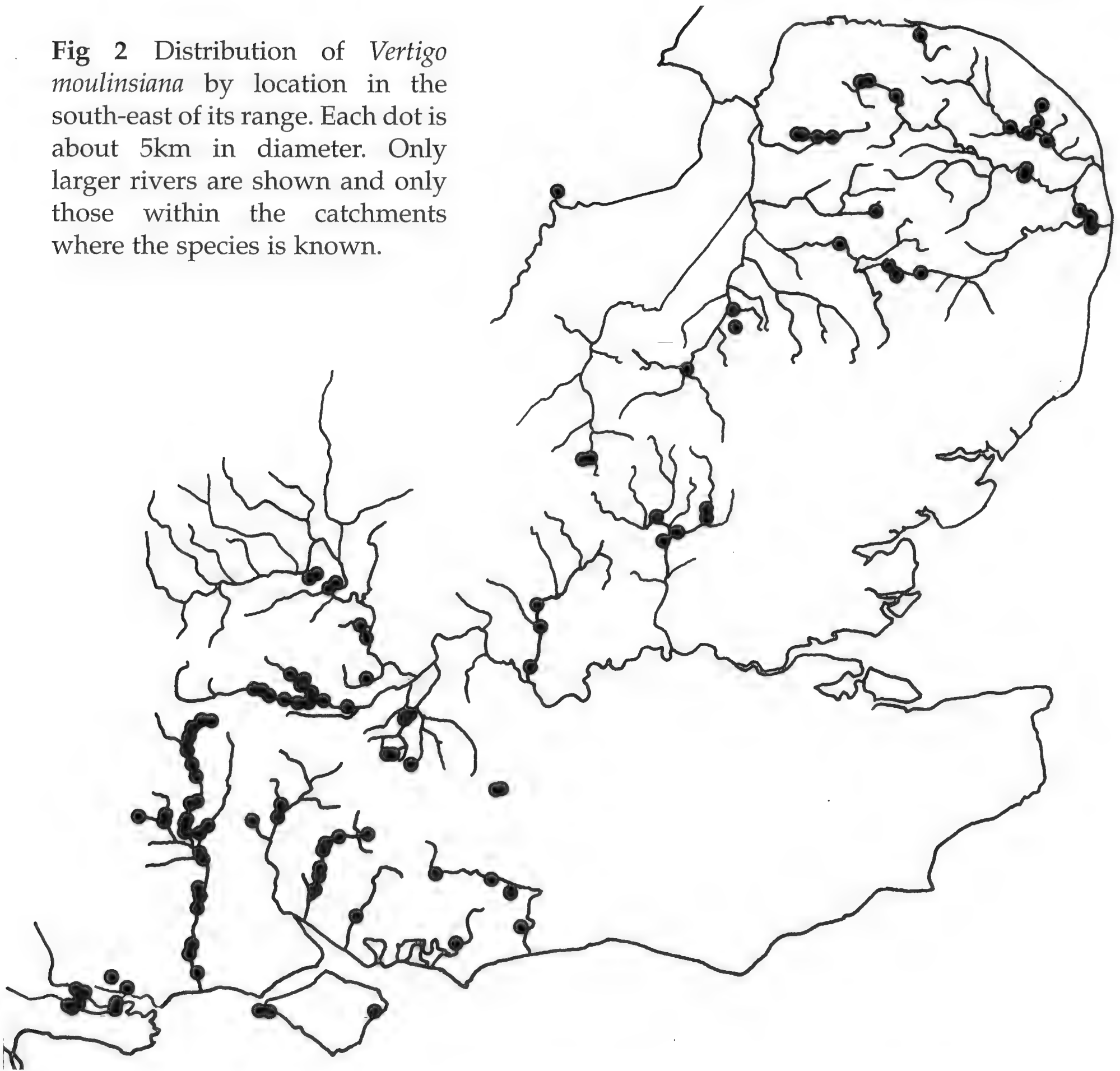
records were obtained through surveys from 1961 to 1976 alone (Kerney, 1976), so *V. moulinsiana* is still a relatively little-recorded species. The frequency with which it has been recorded shows the familiar pattern of enthusiastic late Victorian and Edwardian collecting, the inter-wars lull, a burst of activity leading to the first provisional atlas (Kerney, 1976), and continued high level of recording in response to its recognised value to conservation (Figure 1).

DISTRIBUTION BY 10 KM SQUARE

The first Atlas of terrestrial and freshwater molluscs (Kerney, 1976) gives the distribution of *V. moulinsiana* as a band from Norfolk to east Dorset. The latest Atlas (Kerney, 1999) shows little change to the overall pattern but recent recording has filled in many more squares of the National Grid, especially in the south-west of the range in the 100 km square SU (Berkshire, Hampshire and Wiltshire). The Hertfordshire and Cambridgeshire areas within 100 km square TL continue to show no real increase in the snail's occurrence.

These data do not suggest a contraction in range since 1965 (the year chosen in the 1999 Atlas for 'recent' records), even though a recent targeted survey has clearly biassed the comparison between long periods.

TABLE 1

Number of localities (and records in parentheses) within or outside of Sites of Special Scientific Interest (SSSI) where *Vertigo moulinsiana* has been recorded up to 1999. Uncertain records are close to SSSIs so may have been made within them. The full name of the SSSI is given even though the snail may be absent from some parts of complex sites. * = pre-1970; † = presumed extinct.

County	within SSSI	outside SSSI	uncertain	named SSSI
Berkshire	16 (20)	17 (20)		Boxford Water Meadows, Chilton Foliat Meadows, Freeman's Marsh, Kennet & Lambourn Floodplain, River Kennet, Stanford End Mill & River Loddon*, Thatcham Reed Beds
Cambridgeshire	2 (4)	2 (2)		Sutton Heath & Bog, Wicken Fen
Devon		1(6)		
Dorset	1	14 (16)		Wareham Meadows
Essex	2 (2)		1	Little Hallingbury, Thorley Flood Pound
Greater London	1 (3)	4 (4)		Denham Lock Wood
Hampshire	16 (21)	5 (5)	6 (6)	Avon Valley, Chilbolton Common, Greywell Fen, Itchen Valley (Winchester Meadows), Mapledurwell Fen, River Avon, River Itchen, River Test, Winnal Moors
Hertfordshire	2 (5)	5 (5)		Hunsdon Mead ?*, Sawbridgeworth
Isle of Wight	2 (2)		1 (3)	Freshwater Marshes, Headon Warren & West High Down*
Norfolk	13 (33+)	1	3 (3)	Alderfen Broad*, Ant Broads & Marshes, Bure Marshes, ? Castle Acre Common, East Walton & Adcocks Commons, Ludham to Potter Heigham Marshes*, River Nar, River Wensum, Thompson Common, Upton Broads & Marshes*, Yare Broads & Marshes
Nottinghamshire		1		
Oxfordshire	1 (4)	4 (4)	1	Cothill Fen & Parsonage Moor
Shropshire	1 (2)			Sweat Mere & Crose Mere
Suffolk	4 (11)	4 (4)		Knettishall Heath*, Market Weston Fen, Redgrave & Lopham Fen†, Sprats Water & Marshes*
Surrey	1		3 (3)	Eashing to Charterhouse
West Sussex	3 (3)	3 (5)		Arundel Park, Burton Park, Chichester Harbour
Wiltshire	17 (2)	5 (5)		Jones's Mill, Lower Woodford Water Meadows, Porton Meadows, River Avon
Gwynedd	1			Cors Geirch NNR
total	**84 (133)**	**66 (78)**	**15 (17)**	**52 (including 8 * and 1 †)**

Vertigo moulinsiana has a strong but not exclusive association with calcareous geology. Boycott (1934) placed *V. moulinsiana* within his group of molluscs indifferent to lime but this appears to be an oversimplification. Most sites fall within areas defined as chalk or limestone in overlays of variables produced by the Biological Records Centre (Institute of Terrestrial Ecology, 1978), although there are exceptional sites such as Morden Bog in Dorset, where conditions must be only just basic. The variables of February minimum temperature, January and July average temperatures, and average annual rainfall do not help explain the modern distribution. The current distribution is far smaller than in the species' climatic optimum of the Postglacial period about 5000 BP (Kerney, 1991).

REPRESENTATION ON SSSIS AND SACS

Of the 165 separate localities recognised in the database, just over half occur within existing Sites of Special Scientific Interest (Table 1), represented by 52 separate SSSIs. The colony at Redgrave and Lopham Fen is almost certainly extinct, and a few others have not been re-recorded since 1970. This still leaves a large proportion of presumably extant colonies within 43 SSSIs. The locations for some, mostly old records are too imprecisely given to be sure whether they were made within an area that is now an SSSI (this land designation stems from the 1949 National Parks and Access to the Countryside Act, updated by the Wildlife and Countryside Act, 1981). For the present purpose, a site is taken as a uniquely named locality but it is recognised that some sites may refer to large areas (e.g. the complex of marshes within the Yare Broads and Marshes SSSI), whereas others given separate status here may be parts of one large colony (e.g. some of the sites along the River Kennet and River Avon).

Five candidate SACs have been selected for *V. moulinsiana*: River Avon, Kennet and Lambourn Floodplain, The Broads, Norfolk Valley Fens, and Waveney and Little Ouse Valley Fens. There are records from three other candidate SACs (The Fens, Cothill Fen and the River Itchen) although the presence of the snail was not used in the selection of these SACs. Together, these SACs include 21 SSSI and nearly 50 separate localities where *V. moulinsiana* has been recorded, many since 1970.

DISTRIBUTION WITHIN CATCHMENTS

As the snail is most frequently associated with rivers or fens on river flood plains, it is convenient to describe the distribution within river catchments (Figure 2).

East Anglia

The broads and fens along the Yare, Bure, Thurne and Ant valleys in the Norfolk Broads support several, often large populations. A particularly dense population has been known on the River Yare from Surlingham Fen to Rockland Broad for several decades (Ellis, 1941; Baker & Howlett, 1997). Other sites include Woodbastwick Fen and Upton Broad in the Bure valley, and Alderfen Broad and Sutton Broad in the Ant valley. There is no doubt that this complex is of major importance for *V. moulinsiana* even though its existence here was not recorded until about 1940 when Ellis (1941) described it (and *V. antivertigo*) as "very common in the reed-swamps of East Norfolk".

The valley fens of the upper Waveney and Little Ouse once supported more extensive populations, for example at Redgrave and Lopham Fen National Nature Reserve (NNR), but now the snail appears to be restricted mainly to Market Weston Fen SSSI on a tributary of the Little Ouse, where it is recorded as being "widespread over an extensive area of the fen" (Killeen, 1992a, b). Its loss from Redgrave and Lopham Fen NNR is almost certainly due to ground water abstraction which has caused most of the fen to dry out in the last decade. Of the three known locations along the lower reaches of the River Waveney, Share Marsh and Oulton Broad support large populations of the snail.

Differing markedly from these valley and floodplain fens are the pingo fens of East

Walton & Adcocks Common SSSI and Thompson Common SSSI where extensive populations are found. The pingos are glacial in origin and are associated with only tiny first-order streams which are themselves not important habitat for the snail.

The Cambridgeshire Fens may once have supported an extensive population. Relicts of such a population have been found at river and fen sites. Records suggest that Wicken Fen NNR, where the snail has been known for a century, may have a locally dense population although this site has not been searched thoroughly for the snail in recent years. An isolated record comes from a drain within the arable landscape a few kilometres south of Wicken Fen. Riverside records include an old one (1908) from Grantchester, presumably from close to the River Cam, and from the Little Ouse.

In the chalk streams of north Norfolk, *V moulinsiana* has been recorded intermittently along the rivers Nar, Wensum and Glaven, which represent two catchments. Several of the records fall within the River Nar SSSI and River Wensum SSSI.

East Midlands
A marked outlier from the main pattern of distribution occurs at Sutton Heath and Bog SSSI on the Jurassic limestone in north-west Cambridgeshire. Here a large population of *V. moulinsiana* is found in an area of lightly grazed seepage fen within a few hundred metres of the River Nene whose banks themselves are unlikely to support the snail.

Thames catchment
Many of the tributaries of the River Thames drain the Chalk of central and southern England. These rivers are treated separately since the catchment is vast and the colonies may be effectively isolated despite the hydrological continuity.

Upper Thames
Records were known from south-west of Oxford early in the century (Ellis, 1926), notably from Cothill Fen over the Jurassic limestone where *V. moulinsiana* still occurs. A cluster of colonies has recently been located by or near the River Thames in the vicinity of Wallingford (Cholsey, South Stoke), about 20 km from Cothill Fen, although the fen and river are not linked. The population at Cholsey Marsh appears to be thriving (Graham Stevens, pers. comm.). An isolated record comes from Radley, some 15-20 km downstream of this cluster. Chatfield (1997) concluded that there was little suitable habitat along this part of the Thames, and that even Cothill Fen is drying out to a state where the species is restricted to small wetter areas only.

Kennet and Lambourn (Berkshire)
The snail had been recorded in the 1970s and 1990s at several sites along both of these chalk rivers, sometimes in abundance (e.g. Weideli, 1995). Surveys by Killeen (1996a, d) and Willing (1996) showed that *V. moulinsiana* was present at many sites from Knighton to Brimpton on the River Kennet (a distance of about 26 km) and from Weston to Newbury on the River Lambourn (about 9 km). It was numerous at some of these sites and its frequent occurrence suggested that it was probably present at most suitable patches of habitat along both rivers. The Kennet and Lambourn valleys provide one of the longest and most continuous blocks of habitat suitable for the snail in England.

Pang
There is an old (1906) record from Bradfield on the River Pang, along whose course there is still suitable habitat that may well support the species upstream of Bradfield.

Loddon catchment (Hampshire/Berkshire)
Single sites are known on three different calcareous rivers, two of which are the head-

water fens of the River Whitewater (Greywell Fen SSSI) and Lyde River (Mapledurwell Fen) where small numbers of *V moulinsiana* have been recorded. Three populations are recorded along the upper half of the River Loddon itself or in adjacent fen or wet meadows, and 'reasonable numbers' were found at one site. These sites are not far from the populations on the River Kennet and may be considered part of the Thames Basin catchment.

Wey catchment (Surrey)

A recent record of an extensive but patchily distributed population in the fen alongside the River Wey from Charterhouse to Godalming confirms the continued existence of the snail in south-west Surrey where it was recorded early in the century from Eashing Marsh. A now-extinct colony that once lived at 'hammer ponds' at Hindhead Bottom may also be within the Wey catchment.

Colne (Hertfordshire/Greater London)

Another cluster of old records comes from a short section of the River Colne (a tributary of the River Thames) and the Grand Union Canal which runs alongside the Colne, in the vicinity of Harefield. Kirby (1996) confirmed the continued presence of a small and dense but vulnerable colony which had been last recorded 25 years previously. Downstream, a population in a fen at Denham Lock SSSI may be suffering from drying-out of the site (Plant, 1991).

Lea and Stort catchments (Hertfordshire/Essex)

A cluster of records has been known for many years along these two rivers, the largest and most healthy being that at Sawbridgeworth SSSI on the River Stort. Kirby (1996) discovered two new but sparse populations at nearby fenland SSSIs on this river, Little Hallingbury Marsh and Thorley Flood Pound. Several sites of old records at Rye House and Ware, both on the River Lea, and Roydon on the River Stort (Stratton, 1954) are now thought to be unsuitable for the snail. A further old record was made from Hitchin in the different, north-flowing catchment of the River Ouse.

Rother - Arun catchment (West Sussex)

Populations have been found at Selham Fen on a tributary of the River Rother (Willing, 1991, 1992) and the margins of three large, man-made ponds. The snail has apparently become extinct at Harting Pond but a large and thriving population exists at two linked mill ponds at Burton Park SSSI where extensive reed beds extend onto the ponds as hydroseral succession takes place (Willing, 1992). Swanbourne Lake in Arundel Park SSSI supports a population of unknown size. Willing (1991, 1992) did not locate *V. moulinsiana* at many other wetlands he surveyed in the Rother valley, suggesting that the snail has a restricted distribution in this catchment.

Hampshire Chalk Streams (Rivers Test, Itchen and Meon)

Vertigo moulinsiana was first recorded as British from marsh beside the River Itchen near Otterbourne in 1877 (Groves, 1880). This river, together with the River Test and River Meon, has produced many records over the past 30 years. Additional survey by English Nature on the River Itchen found *V. moulinsiana* at three of nine stations investigated (Chatfield, 1996). As suitable habitat is frequent along the river, more intensive survey will almost certainly show that the snail is more widely distributed here, as confirmed by recent collecting (M. J. Willing, pers. comm.).

Hampshire/Wiltshire Avon

Weideli (1993) published the first record for the upper Avon. Killeen (1996b) recently

showed *V. moulinsiana* to be present at many sites where it is sometimes numerous along the Avon north of Salisbury (a linear distance of about 27 km), and at sites on three main tributaries, the Wylye, Bourne and Till (several kilometres altogether). It is probably present at many suitable patches of habitat here although, compared with the Kennet and Lambourn valleys where agriculture is often unintensive, the patches in the Avon catchment are smaller and more fragmented. However, these rivers still support one of the largest populations of the snail in England. There are both old and scanty recent records (M.J. Willing, pers. comm.) for sites south of Salisbury as far as the Fordingbridge area but at least one old site was thought to have become too dry to support the snail any longer, and others which appeared suitable may have hydrological conditions that are too unstable for the snail (Killeen, 1996b).

Piddle and Frome catchment (Dorset)

Records have been made since 1890 to the present from these two rivers, with rather more records from the mid twentieth century than for many rivers (e.g. Davis, 1957a; Pitchford, 1968). The snail is well established and perhaps widespread in at least the lower reaches of these catchments (M.J. Willing, pers. comm.). Some old records come from the Morden area which is curious in view of the acidic nature of this area, although it is possible that the finds were made close to the chalk just north of the heathland, or that the name was used imprecisely. It is also not clear whether any of the old records were made within areas that are now SSSI; the low proportion of populations within SSSI in Dorset may not be real (Table 1).

Isle of Wight

Preece (1980) mapped the snail's distribution on the island. Here, as elsewhere in the south-west of the snail's range, it has been recorded where freshwater meets the Chalk, although it is now known from only Freshwater and Brading Marshes. One past site was unusual in being apparently tufaceous seepage on coastal slippage, described by Morey (1909) as "at the roots of rushes in a marshy place on the broken ground at Totland Bay", and again by Davis (1957b) as "boggy places on the broken ground forming the cliff at Totland Bay [where] tufa occurs only a few feet above the site where *moulinsiana* still holds a precarious existence".

Devon

At Braunton Burrows, the snail was recorded at marshes behind the dunes for many years in the first half of this century but drainage has made the site unsuitable now.

Shropshire

A tantalising outlier exists at Sweatmere NNR where the single, apparently thriving population is still present in the area of sedges and rushes with developing alder and willow carr, immediately beyond the reed beds that surround the mere. Searches at nearby suitable fens have been unsuccessful in locating more *V. moulinsiana* (Cameron, 1992).

Gwynedd

An unexpected find from calcareous tufa-rich fen at Cors Geirch NNR on the Lleyn peninsular shows how incomplete is our knowledge of the distribution of this species. In 1999 Barry Colville discovered a colony that appears to be thriving and was collected by Adrian P. Fowles (pers. comm.) by beating large clumps of *Cladium mariscus*

Ellis (1926) mentions Keswick in Cumbria as a site. This is an error for *V. lilljeborgi* (Kevan, 1933).

EUROPEAN DISTRIBUTION AND STATUS

The current distribution and status of *V. moulinsiana* in its mainland range is given by Killeen (1996c) and Wells & Chatfield (1992). Butot & Neuteboom (1958) gave a similar distribution some 40 years ago. Additional recent information was obtained by Seddon (1996) by contacting specialists in many European countries to obtain information resulting from the snail having been listed on the Habitats and Species Directive.

Pokryszko (1990) describes *V. moulinsiana* as an Atlantic - Mediterranean species, its distribution encompassed by north-western Europe, Spain, Sweden and Azerbaijan, and possibly Morroco and Algeria (Seddon & Holyoak, 1993). Within this range it is decidedly scarce, and only in two countries other than England are there more than a handful of records. In Ireland, it is locally distributed in the central lowlands (Kerney, 1976; Killeen, 1996c) and several new sites for the snail have been located along the Shannon and Barrow rivers (Seddon, 1996, quoting M. Speight *in litt.*). A moderate number of sites for *V. moulinsiana* is known from Hungary where Pinter *et al.* (1979) record it in 24 10-km squares. Here it appears to occur in a slightly different habitat to that occupied in England. Not only is it viewed as a characteristic montane wetland species but Nyilas & Sumegi (1991) describe it from cool and humid 'birch marshland' (*Betula* and *Salix*) and from an oak *(Quercus)* forest that floods periodically. Bondesen (1966) regards *V. moulinsiana* as being characteristic of 'alder swamps' *(Alnus)* in Denmark. In both Hungary and Denmark, it is not clear whether the snail is found within shade in the woodlands; it seems more likely that it occurs in clearings where fen vegetation grows.

V. moulinsiana remains scarce and possibly declining in other countries. In Belgium, the species was regarded as extinct (Wells & Chatfield, 1992) but recent work targeted at *V. moulinsiana* in response to the Habitats and Species Directive has revealed new sites in a total of five 10 km squares (Seddon, 1996). There is suitable habitat in northern and central France but there have been no recent surveys specifically for this species (Seddon, 1996, quoting Bouchet & Ripken, *in litt.*). France would appear to be under-recorded by its own naturalists, judging from three recent published records which were made by visiting conchologists, all of whom recorded it in habitats similar to those in southern England (Kuiper, 1980; Colville, 1985; Chatfield & Stevanovitch, 1986). The species is considered rare but not endangered in Germany and Switzerland. Much of the decline noted in Poland, Germany, Sweden and the Netherlands is attributed to loss of habitat. *Vertigo moulinsiana* appears to be genuinely scarce in the last two countries where recent conchological surveys have been undertaken in response to of the Habitats and Species Directive. Its status in other countries is given by Killeen (1996c) and Seddon (1996).

Over its entire range, there has been a reduction of about 30-40% in the number of sites occupied since 1930, and, within the European Union, only England and Ireland are known to have reasonable populations (Seddon, 1996).

HABITAT REQUIREMENTS

Killeen (1996c) gave a succinct summary of the snail's ecology and while most of his account remains true, our understanding of some aspects has been modified in the light of more recent studies, most notably its occurrence on recently disturbed habitat.

"The species mainly inhabits calcareous wetlands. In the UK it occurs in long-established swamps, fens and marshes usually bordering rivers and lakes. It lives on both living and dead stems and leaves of tall plants: grasses (e.g. *Glyceria maxima*), sedges such as *Carex riparia* and *Cladium mariscus*, and reeds *(Phragmites australis)*. The species shows a preference for life on taller vegetation on which it ascends during the season, and is rarely found in litter. A similar habitat and ecology is described for [other European countries]."

The habitat details given in the recent surveys and on record cards submitted to the national recording scheme corroborate much of this account. Of half the records for which a substratum was mentioned, large sedges *(Carex)* and *Glyceria maxima* are the most frequently used by the snails, with *Glyceria* being especially important along chalk rivers but mentioned relatively infrequently from Norfolk sites (Table 2). Reed *(Phragmites australis)* is relatively infrequently used, except perhaps along Dorset streams (Davis, 1957) and in Norfolk Broadland, for instance at Surlingham where many individuals can be seen on sparse reed. *Cladium mariscus* is mentioned rarely and only for sites in Norfolk, at Market Weston Fen in Suffolk and Cors Geirch in Gwynedd (Killeen, 1992a, b; A.P. Fowles, pers. comm.), which is unsurprising in view of the sedge's restricted distribution (Perring & Walters, 1990). Tall herbs and tall monocotyledons such as *Typha latifolia* L. and *Iris pseudacorus* are also rarely mentioned on the record cards, although Ellis (1941) recorded *V. moulinsiana* being more common than *V. antivertigo* in what he described as *Typha*-dominated swamp, and Langmead (1946) recorded numerous snails on leaves presumably of *Typha* and *Sparganium* which dominated the swamp at a lake margin. In all the cases where *Phalaris arundinacea* L. is mentioned, it is unclear whether the snails were found on this plant or it is merely included as a component of a rich fen flora. Phillips (1908) recorded snails from dead bur-reed *(Sparganium ?erectum* L.), an observation not repeated in the record cards. Germain (1930) gave *Juncus,* and Pokryszko (1990) gave *Typha* and *Iris.* However, where detailed work has been undertaken, *V. moulinsiana* can be found on a wide range of plants at one site (I.J. Killeen, pers. comm.).

Remarkably few record cards or accounts mention finding *V. moulinsiana* in litter although this may be due simply to such a frequently searched habitat not being recorded, leaving a greater proportion of observations of the less usual leaf-dwelling habit. It does occur in winter in the litter of *Glyceria maxima* after the plants have collapsed (Killeen & Stebbings, 1998) and Pokryszko (1990) stated that the snails spend the winter in the litter layer. *V. moulinsiana* has also been found in litter samples processed in the laboratory when plants have been searched unsuccessfully (Kirby, 1996).

TABLE 2

Substrata on which *Vertigo moulinsiana* has been recorded. Data are from records submitted to the national recording scheme and recent English Nature surveys.

Substrata	Number of records	Percentage	Notes
sedge	49	20.9	includes *Carex paniculata* L., *C. acutiformis* Ehrh, *C riparia* Curt. and unspecified *Carex*
Glyceria	30	12.8	assumed to be *G. maxima* (Hartm.) Holmberg.
Phragmites australis (Cav.) Trin.	20	8.5	
Cladium mariscus (L.) Pohl	4	1.7	
Phalaris arundinacea L.(?), *Typha* spp, *Iris pseudacorus* L., rushes, tall grasses, tall herbs	15	6.4	Uncertain whether snails were found on *Phalaris*
litter, debris	4	1.7	includes flood debris
water or pitfall traps	3	1.3	Norfolk fens
no substrata mentioned	111	47.4	included withy bed and cress bed

Management practices that reduce or eradicate tall monocotyledons are obviously detrimental to the snail. For instance, it is absent where cattle graze the banks of the River Avon (Killeen, 1996b). However, the snail thrives at Sutton Heath and Bog SSSI (Cambridgeshire) in an area subject to light cattle grazing, at Sawbridgeworth Fen SSSI (Essex) where sedges are cut regularly (Kirby, 1996), and at Market Weston Fen SSSI (Suffolk) which has a long history of *Cladium* mowing.

A number of habitats other than those covered by Killeen's account above are given on recording cards. These include shallow wet depressions in meadows (with or without grazing), drainage ditches in pasture, and reedbeds. The inhabited plants are usually standing in shallow water or are on saturated ground, so this will restrict the snail's distribution within sites. This was clearly shown at Bagnor on the River Lambourn where the distribution was plotted accurately within an area of about 40 x 50 m (Killeen & Stebbings, 1997). The snail occurred abundantly where seepages allowed swamp to form locally, but was absent in adjacent dry fen.

Vertigo moulinsiana has a strong preference for open situations. This may be because its food, which consists of micro-fungi, algae and bacteria on the leaves (Bondesen, 1966; Killeen, 1996c), is less attractive or abundant in shade. However, it has been found sparsely within shaded sites, for example Killeen (1992a, pers. comm.) recorded it from a poplar plantation, and along a few ditches shaded by sallow *(Salix cinerea* L.) in the Kennet valley, and Baker & Howlett (1997) found it commonly on *Cladium mariscus* and *Carex* species beneath willow canopies in the Norfolk Broads, provided that the scrub was not so dense as to exclude light. It was present in low numbers on sedges throughout Denham Lock Wood (Middlesex), presumably in shade, although it was abundant in a clearing where sedges dominated (Plant, 1996).

The snails passes the winter gregariously in a variety of sites above ground. Pokryszko (1990) stated that they spend the winter in the litter layer, and recent monitoring of a population on *Glyceria maxima* confirms this (Killeen & Stebbings, 1997). Phillips (1908) could not find the snail in the litter of the *Glyceria* marsh but recorded them on the exposed parts of branches of alder *(Alnus glutinosus* (L.) Gaetn.) 30-60 cm above the ground and in aggregations of 4-20 individuals among loose dry leaves in the forks of branches. He also found them on the dead, stiff stems of *Sparganium ?erectum*. Boycott (1934) says "it sticks itself high up on to the dead flags *[Iris]*, *Glyceria*, etc., and so exposed passes safely through the most severe frosts." Numerous adults preparing to hibernate were found in October, stuck with mucus in the groove formed by dying reed leaves in groups of five to six (Davis, 1957). The snail must presumably be able to withstand immersion for long periods.

Previous accounts of the snail's ecological requirements state that it requires ancient, undisturbed habitat (e.g. Kerney, 1991; Killeen, 1996c). While many of the sites where the snail is found are of high wildlife value and are therefore relatively free from damaging land uses, recent monitoring at the River Lambourn and River Kennet has shown that the snail will occupy and breed readily in translocated and newly created marsh (Killeen & Stebbings, 1998). At the Lambourn site, the snails first continued to breed successfully in translocated 'turves' of *Glyceria maxima* swamp, then rapidly colonised swamp created adjacently by planting individual plants. At the Kennet site, an entirely new scrape was made, fed by river water at one end, and planted with individual plants of snail-free *Glyceria maxima*. By the second summer, *V. moulinsiana* was found in the upstream end of the new swamp up to about 80 m from the river which was the most probable source of the colonists. While these experimental sites are technically disturbed and recent, considerable effort had been made to recreate the habitat where *V. moulinsiana* was found on the flood plain. However, similar patches of swamp must continually form along these and other chalk rivers, since it is frequently removed as part of normal riparian management. As the snail has been recorded in most suitable patches

of such river-side swamp, the supposed need for undisturbed habitat appears to be a simplification.

<div align="center">LIFE CYCLE</div>

The life cycle of *V. moulinsiana* has not been studied in detail but that of *V. pusilla* is described by Pokryszko (1990, 1992). This species reproduces mainly in spring and early summer and, in captivity, snails reach sexual maturity within 30-40 days after hatching, so that adults and juveniles are found together for long periods of the year. Most individuals lived for 10-15 months (exceptionally 17 months). For *V. moulinsiana*, the distribution of dates on 83 record cards where the month was given shows that it is adult, or at least large enough to be identified, throughout the year. Butot & Neuteboom (1958) found young snails in October in the Netherlands, and Phillips (1908) found both large and young snails with 2-3 whorls in January in Ireland. More recent work shows that individuals with from 1½ to 5 whorls can be found together from October to December on the River Lambourn and Kennet (Killeen & Stebbings, 1997; Stebbings & Killeen, 1998). These authors suggest that *V. moulinsiana* may breed opportunistically as weather conditions and food availability permit.

<div align="center">DISCUSSION</div>

This review confirms that *Vertigo moulinsiana* is a scarce species with a restricted English distribution although it fares better than previously thought. The snail occupies a tightly defined habitat. The principle limiting factor appears to be the need for high humidity which may be necessary for the growth of its microbial food. This need can be met by living in fens or next to rivers. Most of the English sites are close to or beside rivers, or in wetlands intimately connected with the water table. Even here, the snails live in the wettest areas where the tall plants on which they live are standing actually in water or in saturated ground. These requirements were recognised over a century ago by Groves (1880) who first discovered the species in England.

Vertigo moulinsiana was given the Red Data Book status of rare (RDB3) on the basis that its habitat is known to be declining, and that several populations have gone extinct as a result (M. Kerney, 1991, and pers. comm.). It is almost certain that the habitat of *V. moulinsiana* is less frequent now than before the last war as a result of drainage, groundwater abstraction, river engineering and possibly loss of tall bankside vegetation resulting from mowing or intensive grazing. The scarcity of recent records for riparian sites in counties just north of the Thames Basin where the snail was previously more widely recorded may be a direct result of such activities. However, the scale of the decline cannot be accurately assessed. It is not possible to use the results of recording over successive periods to demonstrate whether a species is declining because recording effort for most invertebrate groups has accelerated in recent decades (for example see Figure 1). *Vertigo moulinsiana* may well have been under-recorded for several reasons. Not only is it very small but its foliage-dwelling habit is unusual among small snails, leading it to be overlooked unless beating and sweep netting are used (methods not often used by conchologists). Recently, surveyors have been successful in finding the snail because of the concerted effort in response to the Habitats and Species Directive, the use of methods that target the species effectively, and surveying habitats along rivers of recognised conservation value where there was a high probability of finding it.

A consequence of focusing attention on this species is that it has been found to be more frequent than previously thought, so that it does not meet an important criterion for inclusion in the British Red Data Book (that a species is thought to occur in 15 or

fewer 10-km squares of the National Grid). If the status of *V. moulinsiana* was revised using the old criteria, it would be classed as Nationally Scarce (that is, found in 16 to 100 10-km squares; Ball, 1994). However, the Joint Nature Conservation Committee, which is responsible for determining statuses, would probably review statuses for Britain using the latest IUCN criteria. It is quite possible that *V. moulinsiana* would qualify as Conservation Dependent, which is the status likely to be assigned in the international assessment currently in progress (M. Seddon, pers. comm.). This is below the two main categories of threat (Vulnerable and Endangered) but is given to a species whose continued existence depends upon conservation action which, if relaxed, would result in it being reclassified as Vulnerable or Endangered. However, until JNCC undertakes a national review of molluscs, the published status for *V. moulinsiana* stands.

Using a crude measure of distribution can lead to a misleading view of a species' well-being. Despite the wide distribution of *V. moulinsiana* suggested at a resolution of 10 km (Kerney, 1999), the snail is confined to very narrow strips of habitat at most of its sites, so the total area occupied is minute. A similar disparity of perception has been noted for Silver Spotted Skipper butterflies when the scale of distribution mapping is altered (Thomas & Abery, 1985). In view of the international status of *V. moulinsiana*, it is important that sufficient of its sites are given legal protection and that appropriate management takes place where this does not compromise conservation interests of greater importance, both within and outside of protected sites. Perhaps because of its propensity to occupy habitat of high quality, the snail receives considerable indirect protection within 43 SSSIs where it has been recorded since 1970. At least 11 of these are managed by conservation organisations. Another 50 or so localities in 21 SSSIs fall within eight candidate SACs which include examples from fen or swamp fringing water-sides and within closed basins. These almost encompass the snail's range in England and include two of the largest populations known (Drake, 1997).

Vertigo moulinsiana has been described as an indicator of ancient undisturbed habitats and its sensitivity to disturbance of such habitat was one of the factors in its inclusion in the Habitats and Species Directive. An indicator of such conditions would be expected to have high fidelity to its habitat and low mobility so that it is rarely encountered in the 'wrong' habitat. High fidelity is shown by the closely defined habitat occupied and by its occurrence in sites of predominantly high conservation value for other organisms. Another expression of fidelity is the snail's continued survival in tiny isolated pockets of suitable habitat, for example one locality on the River Colne where it has been found again at the same short stretch of sedge after 25 years (Kirby, 1996). However, it is clear that the snail does live in patches of habitat that would not have been suitable only a few years previously, as shown in its colonisation of habitat newly created especially for the snail along the River Kennet and River Lambourn. Local colonisation and extinction are inevitable along rivers where riparian management involves periodically clearing stretches of marginal vegetation.

Wells & Chatfield (1992) and Kerney (1991) summarised the threats to *V. moulinsiana*. These are lowering water levels through drainage and ground-water abstraction, riparian engineering, mowing river meadows, and cultivating or reclaiming fens. Other threats listed by authors quoted by Wells & Chatfield (1992) include nutrient enrichment and infilling of ponds. Intensive grazing of unfenced river margins has been identified as a threat on chalk rivers in Hampshire and Wiltshire as this removes tall riparian vegetation, although *V. moulinsiana* can clearly tolerate light grazing and traditional sedge mowing. Initial measures to protect this species must address factors that result in lowering of water levels and complete loss of the tall vegetation. At sites with extensive populations, for example the Hampshire and Wiltshire chalk rivers, local extinction resulting from riparian management or changes in the stocking density of grazing animals has probably been a feature for many decades so there is probably no cause for

serious concern with current practices. Large and extensive changes in these practices would need to be addressed since the species is thought to have limited powers of dispersal and colonisation.

There is no information on the mobility of these small snails but it may be speculated that they could be moved during floods or by sticking to the plumage of water fowl as they push through marginal vegetation. Support for the idea that the snail can disperse, perhaps moderately readily, along rivers comes from finding *V. moulinsiana* at many apparently suitable patches of habitat along the recently well surveyed rivers, and from the rapid establishment of colonies on newly created swamp. If there is some interchange of individuals between sites along a river, then each river or catchment may represent a single population. Dispersal primarily along river corridors may lead to populations within a catchment being effectively isolated from each other, even though separated by only a short distance across a watershed. This was an important consideration in selecting two river catchments, the Kennet and Lambourn, and the Avon, as SACs for the snail in the south-west of its range.

The management requirements for the snail should include:
- ground-water reaching the surface for most of the year;
- high humidity retained by dense, tall monocotyledons, preferably *Glyceria maxima*, large *Carex* species, sparse *Phragmites* and *Cladium mariscus*; the replacement of these species by plants of drier conditions, such as *Epilobium hirsutum* or *Urtica dioica*, indicates that conditions have become too dry;
- limiting disturbance of river-side or fenland vegetation, for example by instigating rotational clearance of short stretches of riparian vegetation;
- preferably no mowing or grazing, particularly in sites where there is no history of these activities. If mowing has taken place for many years and the snail persists, it should be done in blocks smaller than the patch of suitable habitat; this will allow the snail to re-colonise from adjacent blocks when the vegetation recovers. Light grazing that does not suppress tall monocotyledons is acceptable.
- unshaded or only lightly shaded conditions; some patchy sallow or alder scrub may provide winter refuge from high water levels.
- calcareous water supply.

ACKNOWLEDGEMENTS

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SINUM BIFASCIATUM (RÉCLUZ, 1851) (GASTROPODA: NATICIDAE) CONFIRMED IN MEDITERRANEAN FAUNA

The large Naticid *Sinum bifasciatum* (Récluz, 1851) has a mainly tropical West African distribution, but was reported in the Mediterranean by XIX century authors. These records are often ignored today or considered spurious, but here we report on well established populations on the coast of Malaga, and some modern records of the species which confirm *Sinum bifasciatum* as a member of the Western Mediterranean fauna.

Early records, under the name *Sigaretus haliotideus* (Linné, 1758) go back to Ramis[1] for Menorca, and Payraudeau[2] for Corsica. Philippi[3] mentioned a specimen from bay of Taranto, received from Costa and later[4] figured it. MacAndrew[5] recorded the species from S. Portugal and Malaga, Weinkauff[6] from Algiers and Hidalgo[7] mentioned a fresh shell from Menorca, collected by Cardona.

Weinkauff[8] first questioned that the Linnean name was appropriate for the Mediterranean species, and used a name established for a Miocene fossil, *Sigaretus striatus* (de Serres, 1828). He later[9] proposed the name *Sigaretus philippii* Weinkauff, 1883, based on the Mediterranean specimen figured as *S. haliotideus* by Philippi[4]. *Sigaretus bifasciatus* Recluz, 1851, described from São Tomé[10], is an earlier specific name for this species and should be used.

The mediterranean occurrence of *Sigaretus* was disputed by Monterosato[11] and, possibly following this influential paper, the species was virtually ignored or records were distrusted. The few exceptions include Hidalgo[12], who reported "*Sigaretus philippii Weinkauff*" from Faro, Setubal, Cadiz, Malaga, Menorca, rare on the beach, and Nobre[13] who reported original material from several localities in Southern Portugal. Spada & Maldonado Quiles[14] mentioned 3 specimens from Fuengirola (Malaga province, Spain) but were reluctant to accept this as evidence that the species lives there. The entries in the review of Schiró[15] and in the catalogue of Sabelli *et al.*[16] are also given with reservations. Most contemporary identification guides ignore the species, with the exception of Poppe & Goto[17] who state its occurrence as "rare" and "probably limited to the Alboran Sea", but do not give details of records.

We have encountered living specimens of *Sinum bifasciatum* in material coming along with commercially dredged "coquina" (*Donax trunculus* Linné, 1758) on shallow sandy bottoms (2-6 m depth). The dredge is equipped frontally with a rake digging some 10 cm in the sand, and has a mesh of 1.5 cm. The benthic community corresponds to the "sables fins bien calibrés" (SFBC) of Pérès & Picard[18].

The following material was examined. (All measurements are length x width):
Fuengirola 6-10 July 1987: 1 specimen (dimensions of shell 34 x 24 mm).
Torre del Mar/Benajarafe, July/November 1998: 9 specimens (dimensions of shell: 33 x 23 mm, 31 x 23 mm, 30 x 22 mm, 29 x 24 mm, 27 x 20 mm, 27 x 19 mm, 26 x 19 mm, 24 x 18 mm, 22 x 17 mm) and one shell (30 x 21 mm).

The fisherman who communicated the latter material stated that it is regularly found in the catch and purchased by collectors at a price rounding one dollar per specimen. He knows it under the colloquial name "manteca" (spanish for "grease", allusive to the aspect of the whitish translucent living animal).

The second author also collected this species on the Moroccan coast (1 shell on the beach of Tangier, 1971, and one shell at the mouth of the Bou-Regreg, Rabat, 1972).

These occurrences confirm *Sinum bifasciatum* as an established species in the fauna of the Alboran Sea. The large, multispiral protoconch in this species indicates a plank-

totrophic larval development, and this is consistent with the extensive range (from Alboran Sea and Southern Portugal to Angola, and the islands of the Gulf of Guinea) in which it is known.

The older records suggest a broader range, spanning virtually the whole Western Mediterranean, but it is not possible to say whether this means that the range has really been broader in former times, or if specimens were mislabeled or misidentified. The lack of modern records for Algeria, Corsica or the Baleares can be explained by a lack of collecting, but this cannot be said for the Italian type locality of *Sigaretus philippii*.

[1] RAMIS J. 1814 *Specimen animalium, vegetabilium.. in insula Minorica frequentiorum.* Magone Balearium [Mahón]: 608.

[2] PAYRAUDEAU B.C. 1826 *Catalogue descriptif et méthodique des Annelides et des Mollusques de l'île de Corse:* 121 (n° 255).

[3] PHILIPPI R.A. 1836 *Enumeratio molluscorum Siciliae* Berlin: 165.

[4] PHILIPPI R.A. 1844 *Abbildungen und Beschreibungen neuer oder wenig gekannter Conchylien* T. Fischer, Cassel. Vol.1: 144, pl. 1 fig. 6.

[5] MACANDREW R. 1857 *Reports of the British Association for the Advancement of Science* (1856): 126.

[6] WEINKAUFF H.C. 1862 *Journal de Conchyliologie* **10**: 347.

[7] HIDALGO J.G. 1867 *Journal de Conchyliologie* **15**: 366.

[8] WEINKAUFF H.C. 1867-1868 *Die Conchylien des Mittelmeeres, ihre geographische und geologisches Verbreitung* T. Fischer, Cassel Vol. **2**: 259-260.

[9] WEINKAUFF H.C. 1883 *Die Gattung Sigaretus. In: Systematisches Conchylien-Cabinet von Martini und Chemnitz, 2nd edition* Bauer & Raspe, Nurnberg Vol 6 (1), pl. 5 fig. 1-3.

[10] RÉCLUZ C.A. 1851 *Journal de Conchyliologie* **2**: 190, pl. 6 fig. 3-4.

[11] MONTEROSATO T.A. DI 1878 *Giornale di scienze naturali ed economiche di Palermo* **13**: 97, footnote 1.

[12] HIDALGO J.G. 1916 *Fauna malacologica de España, Portugal y las Baleares. Moluscos testaceos marinos* Museo Nacional de Ciencias Naturales, Madrid: 634.

[13] NOBRE A. 1940 *Fauna malacologica de Portugal. I. Moluscos marinhos e das aguas salobras* Editora do Minho, Porto: 337-338.

[14] SPADA G. & MALDONADO QUILES A. 1974. *Quaderni della Civica Stazione Idrobiologica di Milano* **5**: 58-59.

[15] SCHIRÓ G. 1978 *La Conchiglia* **106-107**: 8-10.

[16] SABELLI B., GIANNUZZI-SAVELLI R. & BEDULLI D. 1992 *Catalogo annotato dei Molluschi marini del Mediterraneo* Libreria Naturalistica Bolognese Vol. **2**: 385.

[17] POPPE G.T. & GOTO Y. 1991 *European Seashells* Christa Hemmen, Wiesbaden. Vol. **1**: 120.

[18] PÉRÈS J.M. & PICARD J. 1964 *Recueil des Travaux de la Station Marine d'Endoume* **47**: 57-58.

J.L. Rueda and S. Gofas
Dept. Biología Animal
Facultad de Ciencias
Universidad de Málaga
E29071 Málaga
Spain.

CORBICULA FLUMINEA (MÜLLER): NEW TO U.K.

The Asiatic clam *Corbicula fluminea* (Müller) is a bivalve species of eastern Asia; Philippines, China, Japan. It was reported in the Ohio River Basin USA in 1957 where it spread at a phenomenal rate over the whole drainage system. In Europe it is now known from the Upper Rhine in Germany, The Lower Rhine in The Netherlands, Portugal and France.

In Taiwan it is known from substrates of sand and mud or a combination of the two but with a preference for sandy substrates rather than muddy ones. In California Ingram[1] (1959) gives the habitat as sand and mud. The discovery of the bivalve in the River Chet in the southern Norfolk Broads in October 1998 is the first record from the U.K. The River Chet is a small canalised tidal river linked to the larger River Yare. For much of its length the river is banked by wooden and metal pilings and only on some stretches are there any marginal reed-sedge ronds.

Six specimens of *Corbicula fluminea* were collected in depths of 1–2m in silty-sands beyond the common reed margins of the river. Chloride analysis of the water on the high flooding tide showed levels of 460mg/l Cl⁻ at Hardley Hall and 220mg/l Cl⁻ further up river near the Hardley Flood outlet.

The size range of the bivalves collected suggests at least three age groups but since the numbers sampled were small this requires further study. However, it may tentatively be observed that the clam has lived in the River Chet for upwards of four years.

Speculation on its origin in the U.K. ranges from ship freshwater ballast, pleasure craft crossing the North Sea from the Netherlands, wildfowl and even possibly koi carp in the aquarium trade.

[1]INGRAM W.M. 1959 *Journal of the American Water Works Associates* **51**: 363–370.

Derek Howlett and Roy Baker
The Ted Ellis Trust
Wheatfen Broad
Surlingham
Norfolk NR14 7AL

NEW RECORDS OF *PALUDINELLA LITTORINA* FROM CORNWALL, SCILLY AND BRITTANY

Fieldwork during 1998 and 1999 as part of the DOMMIC project (**D**istribution **o**f the **M**arine **M**olluscs **i**n the **C**hannel) has included specific searches for the prosobranch *Paludinella littorina* (delle Chiaje, 1828). This has yielded new living records (9 sites) from Cornwall, the Isles of Scilly and Brittany in northern France:

Cornwall - 2 sites   Poldhu Cove, north of Mullion, Lizard peninsula.
                            Pont Pill, Fowey estuary (fresh shells only).

Isles of Scilly - 6 sites   St Agnes, Gugh, Tresco and St Mary's.

Brittany - 1 site   St Suliac, Rance estuary, south of St Malo, Côtes-d'Armor.

Both Cornwall and the Scillies have long been popular locations for molluscan studies. However, the only previous records for Cornwall are based upon dead shells from Sennen Cove (Land's End) and the Lizard (Marshall 1913[1]). Turk & Seaward (1997[2]) list over 400 species from the Isles of Scilly, yet this does not include even a dead shell of *P. littorina;* a rather surprising fact in light of the recently recorded frequency of the species. Indeed, this recent work has indicated that the Scillies may be a stronghold for *P. littorina* in southern England. We have been unable to trace any previous records from northern France, so the St Suliac record may be the first.

These new sites broadly cover the range of habitats in which *P. littorina* is usually found at the northern limit of its range. At Poldhu Cove it was living in an upper shore cave. The habitat at the Fowey and St Suliac sites consists of upper shore interstitial pebbles and gravels in an estuarine environment. At St Suliac *P. littorina* was living with *Truncatella subcylindrica,* the latter is also known in the Fowey estuary from dead shell records. On the Isles of Scilly *P. littorina* was found at several locations in a well-defined part of the supra-littoral zone, amongst granite chippings and small pebbles with organic detritus below larger, semi-embedded slabs.

Our studies on this species have demonstrated that although *Paludinella* is a south-western species in Britain, and is commoner than previously believed, there are still large gaps in our distributional knowledge. Information in published conservation literature on the species' ecology is, to a large extent, based upon the Fleet population and, therefore, does not have a wide application for species' conservation and site management elsewhere. Further work is required to provide a more comprehensive picture of the true distributional range of *P. littorina* in Britain allowing a more informed Conservation and Management policy to be developed, particularly with respect to candidate Special Areas of Conservation (SAC). The data would also allow the species' status on the Wildlife & Countryside Act to be re-assessed at the next quinquenniel review.

[1]MARSHALL J.T. 1913 *Journal of Conchology* **14**: 65–77.
[2]TURK S.M. & SEAWARD D.R. 1997 *Journal of Natural History* **31**: 555–633.

Ian Killeen   Janice Light
163 High Road West   88 Peperharow Road
Felixstowe   Godalming
Suffolk   Surrey
IP11 9BD   GU7 2PN

CONCHOLOGICAL SOCIETY OF GREAT BRITAIN & IRELAND

REPORT OF THE COUNCIL 1998-1999

The Society announced with regret the deaths of three members, Miss J M Blyther, SRN, SCM, member since 1963: Dr D A A Whiteley, PhD, member since 1989 and Captain W E Owen, Mastermariner, Life Member since 1973.

Council Positions

Mr Brian Eversham began his second year as President of the Society. New Ordinary Members of Council for 1998/9 were Dr Rundle, Mr Gillard and Mr Brown. Mr Aldridge, Mrs Platts and Dr Bishop began their second year on Council; Mr Killeen, Mrs Weideli and Ms Chesney began their final year on Council. Ms Trew was elected Hon. Treasurer, but the post of Hon. Programme Secretary was unfilled. Some preliminary work in producing a programme for 1999 had been undertaken by Ms Reynolds but in November Mrs Weideli agreed to take over as Acting Programme Secretary. Mrs Weideli has produced a full programme for 1999 and although not formally elected until the AGM today the Hon. Programme Secretary's Report is to be presented by her. Ms Trew had been taken ill in the latter part of 1998 and therefore had been unable to fulfil her duties as Hon. Treasurer. Mr Weideli had once more agreed to complete the Society's accounts for the year ending 1998. As news of the seriousness of Ms Trew's illness had not reached Council when the ballot papers were prepared the Society is now seeking an Acting Treasurer for the forthcoming year. All other Council positions remained unchanged.

Publications

Three issues of the *Journal of Conchology* (Volume **36**:2–4) were published, and in addition the *Journal of Conchology Special Publication No 2, Molluscan Conservation: A Strategy for the 21st Century*, edited by I J Killeen, M B Seddon and A M Holmes, was distributed in August. Other forthcoming changes to the *Journal of Conchology* were agreed by Council. These were that the name of the Society should be removed from the front cover (it would still appear on the inside cover) and be replaced by the words 'Molluscan conservation, biogeography and taxonomy'; that the colour of the cover and the species illustrated should be changed, and that up to four colour plates would be included in each issue of the *Journal*. These changes would be implemented with the advent of Volume 37, although some colour plates have already been used. Dr Oliver also proposed the production of a flier to solicit new authors and papers on the subjects of molluscan conservation, biogeography and taxonomy. Four issues of the Conchologist's Newsletter were published (Volume **9**, Part 1, Numbers 145-8). A new membership leaflet and application form was produced in June. Guidelines for the new 'Papers for Students' had been produced, and Dr Kerney's *Atlas of the Land and Freshwater Molluscs of Great Britain & Ireland* is to be published within the next month. A special offer pre-publication price had been offered to members of the Society by the publishers, Harley Books.The Society also published the Annual Programme Card and revised Membership List, rules and mail order form in January 1999.

Changes to Society Rules

At the last Annual General Meeting two changes to the rules were agreed. The proposed

change to Rule 9 was circulated to the members with the AGM ballot paper and agenda and agreed at the meeting by a majority at the 1998 AGM. The change to the rule is as follows with the changes in italics: '9. Second sentence ....The Presidency shall be tenable for not more than *three* years in succession and the President is expected to deliver at least one address.' Additionally a change to rule 18 was proposed and agreed at the AGM, at which the Hon. General Secretary explained that the proposed change was to bring the Society's Rules in line with the Charity Commission rules. This was also agreed by the meeting. The change to the rule is as follows with the changes in italics: '18. The accounts, before being presented, shall be *examined* by *one* examiner usually appointed at the previous Annual General Meeting'. The revised rules were submitted to the Charity Commissioners in March 1998.

Other Council Matters
Five Council meetings were held, and in addition there were three meetings of the Publications Committee. A preliminary meeting to discuss the formation of a 'conservation committee' was held and this committee was christened the Molluscan Conservation Group of Britain & Ireland and had its first formal meeting in November. In November it was decided to reduce the number of Council meetings to four per year, excepting cases of urgency. In May the Society agreed to purchase a computer, peripherals and software for the purpose of creating a computerised database for the Society's Marine Recording Scheme. Council discussed the possibility of creating a Society Website, and Dr Aldridge agreed to take responsibility for this project. The past year seems to have been a particularly hectic one for the Hon. General Secretary, as there have been additional duties associated with the lack of Hon. Programme Secretary and Treasurer for at least part of the time. This was compounded by the fact that the Secretary's computer blew up (literally!) at the time the January mail out was being prepared. As a result of this Council decided to make an allowance in the accounts for repairs and replacement of both Society owned computers. I am especially grateful to Mr & Mrs Michael and Helen Weideli without whose help the Society would not function, and for their personal support. Thanks also to all the other members of Council who have worked hard over the past year, and to Miss Nelson, Mrs Pain and Miss Fogan who have dutifully produced the teas.

Ms J.E. Reynolds
Hon. General Secretary
March 1999

TREASURERS REPORT 1998

Format of the Accounts
The format of the accounts has been changed in order to more accurately reflect the Society's financial position and to make it easier to understand. The Research and Reserve fund, the Life Membership fund and the Capital Account have now been amalgamated as "Society Reserves". The small fund intended to cover possible damage to field meetings equipment while on loan to the Society has now been included as a provision.

During the year the Society purchased a computer for the recording of marine data and authority was given by Council to provide for the replacement in 1999 of the computer used by the Secretary. It has been decided to show these purchases as fixed assets and not to write them off in the year of purchase.

Income
Income from subscriptions was £11,030 which is £375 less than in 1997. This is partly because covenant income has reduced following the lapsing of most of the 4 year covenants and partly because of reduced membership. Efforts made to secure new covenants for future years have been very successful and income from this source should be restored in 1999

Sales
Sales of back numbers and other publications continue to be a useful source of income. Income now includes the sales of Special Publication Number 2.

Publications
The cost of publishing and distributing the *Journal of Conchology* and the *Conchologist's Newsletter* has not changed significantly. The £11,461 includes the additional cost of printing and distributing *Special Publication No.2.* which was sent free to all fully paid up members and subscribers. Most of the costs for this publication were covered by income received from the Cardiff Conference and its sponsors and was provided for in 1997.

Investments
At the year end the cumulative cost of the investments was £31,458. This is a reduction of £800 resulting from the redemption of *Treasury Stock 1998* which matured during the year. The market value of these investments at 31 December 1998 was £72,658 and in accordance with the policy introduced last year this is the value shown in the balance sheet. The revaluation surplus of £4,089 has been added to the Society Reserves.

Fixed Assets
The Fixed Assets entry of £3,000 which appears in the balance sheet includes £2,500 for the marine data hardware less £500 depreciation in 1998, plus £1,000 for the new machine for the Secretary which it is intended to purchase in 1999. We intend depreciating computers over five years from the date of purchase.

Movement in Reserves
The reserves have been increased as follows:
- £909 from 1998 profit.
- £230 from transfer from the Life Membership fund following a reduction in the number of Life Members.

• £4,089 from the increase in the Market value of the Investments.

Membership
At the end of the accounting year membership of the Society stood at 363. This includes 39 Institutes. During the year 18 new members were recruited which partly offset the loss resulting from resignations and unpaid subscriptions, leaving a net loss of 13 members (4 institutions and 9 personal). In the period 1994 to 1998, 102 members were recruited of which only 54 remained paid up members at the end of 1998.

Summary
In summary, the society remains in a good financial position, though the loss of members over the past year is of some concern . With Net Current Assets of £3,774 and Investments totalling £72,658 it is recommended that subscription should be held for the foreseeable future, and that consideration is given to ways of using the funds to improve membership retention and recruitment

Michael Weideli
Membership Secretary and Acting Treasurer

CONCHOLOGICAL SOCIETY OF GREAT BRITAIN & IRELAND. ACCOUNTS FOR THE YEAR ENDED 31 DECEMBER 1998

INCOME AND EXPENDITURE ACCOUNT

	31 Dec. 1998 £	31 Dec. 1997 £
Income		
Fees and Subscriptions	11,030	11,405
Investment Income	3,902	3,749
Sales and Donations	1,248	2,232
Special Events Income	0	2,434
	16,180	19,820
Expenditure		
Publication Costs	11,461	9,236
Stationary & Sundry Postage	1,776	746
Meetings	805	900
Sundry Costs	730	747
	15,272	11,629
Profit for the year	908	8,191
Movement in Reserves		
Society Reserve Brought Forward	74,205	57,063
Profit for the year	908	8,191
Transfer from Life Membership Fund	230	0
Increase in Market Value of Investments	4,089	8,951
Society Reserves Carried Forward	79,432	74,205

BALANCE SHEET

	31 Dec. 1998 £	31 Dec. 1997 £
Current Assets		
Cash at Bank	14,500	18,730
Debtors	654	1,089
	15,154	19,819
Current Liabilities		
Creditors and Accrued Charges	6,800	6,868
Subscriptions in Advance	564	461
Life Membership Fund	2,760	2,990
Other Provision & Reserves	1,256	4,664
	11,380	14,983
Net Current Assets	3,774	4,836
Investment - at Market Value	72,658	69,369
Fixed Assets - Computer Equipment	3,000	0
Net Assets	79,432	74,205
Represented by:		
Society Reserves	79,432	74,205

M.D. Weideli   N. Light
Acting Treasurer   Hon. Examiner

REPORT OF THE TRUSTEES FOR 1997 AND 1998

1. The official name of the charity is:
The Conchological Society of Great Britain and Ireland.

2. Working names for the charity are:
The Conchological Society or "Conch Soc".

3. The charity's Registered Number is 208205.

4.The official address is:
(Honorary Secretary Ms J Reynoids)
21c Loraine Rd
Holloway
London
N7 6EZ

5. The objects of the Charity's constitution are:
To promote for the benefit of the public the study of Mollusca in its widest aspects.

6. The Trustee's names are
B Colville and D C Long.

7. The body entitled to appoint trustees is:
Council of the Conchological Society of Great Britain and Ireland.

8. Brief review of the main activities and achievements of the society in relation to its objects:
The Society promoted knowledge of Mollusca through indoor meetings with lectures (5 in 1997, 6 in 1998), workshops (3 in 1997, 3 in 1998), and field recording meetings (6 in 1997, 9 in 1998) either in furtherance of its marine and non-marine mollusc distribution recording schemes for Britain, Ireland and surrounding seas or, in one case, to study fossil molluscs. In 1997 there was a joint meeting on historical malacology with the Malacological Society of London, the Linnean Society and the Society for the History of Natural History. The Society published a quarterly Newsletter, 3 parts of the Journal of Conchology (one in December 1997, 2 in 1998) and a Special Publication covering the Proceedings of the first Molluscan Conservation Conference held in November 1996 in Cardiff. Good progress was made by the Hon. Non-Marine Recorder, in conjuction with Harley Books and the Institute of Terrestrial Ecology, towards publication, expected in early 1999, of a new non-marine mollusc distribution atlas for the British Isles and Ireland. The Hon Conservation Officer has co-ordinated the provision of molluscan conservation advice to organisations and individuals and has provided molluscan conservation-related news items to the British Wildlife magazine.

9. Signature of the trustee authorised to sign the report

(B Colville) Date: 17.2.1999

1997 Tax and Dividends from Conchological Society Investment

	Tax £	Net Dividend £	Tax £	Net Dividend £
M&G Dividend Fund 5080 Units	128.47[1]	513.86	99.30[2]	397.21
Save and Prosper Smaller Companies Income Fund 1620 Units	13.53[3]	54.29	0.07[1]	45.76
Treasury Stock 1998 151/2% £800	12.40[5]	49.60	12.40[6]	49.60
Whitbread 71/4% Loan Stock 1999 £2340	16.97[7]	67.85	16.97[8]	67.87
Mersey Docks & Harbour Board Co OS 436	9.54[9]	38.15	4.91[10]	19.62
Treasury Stock 2006 73/4% £8270	64.09[11]	256.37	64.09[12]	256.37
Royal Bank of Scotland Group plc 1700 OS	56.10[13]	224.40	26.35[14]	105.40

National Savings Income Bond monthly

1998 Tax and Dividends from Conchological Society Investments

	Tax £	Net Dividend £	Tax £	Net Dividend £
M&G Dividend Fund 5080 Units	120.68[15]	577.22	104.33[16]	417.32
Save and Prosper Smaller Companies Income Fund 1620 Units	9.33[17]	37.31		
Treasury Stock 1998 151/2% £800	12.40[18]	49.60		62.00[19]
				800.00[20]
Whitbread 71/4% Loan Stock 1999 £2340	16.96[21]	67.86	16.97[22]	67.85
Mersey Docks & Harbour Board Co OS 436	10.90[23]	43.60	5.45[24]	21.80
Treasury Stock 2006 73/4% £8270	64.09[25]	256.37	64.09[26]	256.37
Royal Bank of Scotland Group plc 1700 OS National Savings Income Bond monthly	64.60[27]	258.40	30.30[28]	121.21

[1] 2/1/1997
[2] 1/7/1997
[3] 31/3/1997
[4] 15/11/1997
[5] 30/3/1997
[6] 30/9/1997
[7] 9/5/1997
[8] 6/11/1997
[9] 6/5/1997
[10] 30/10/1997
[11] 8/3/1997
[12] 8/9/1997
[13] 20/2/1997
[14] 18/7/1997
[15] 2/1/1998
[16] 1/7/1998
[17] 31/3/1998
[18] 30/3/1998
[19] 30/9/1998
[20] Redemption
[21] 5/5/1998
[22] 6/11/1998
[23] 23/4/1998
[24] 29/10/1998
[25] 8/3/1998
[26] 8/9/1998
[27] 19/2/1998
[28] 17/7/1998

RECORDER'S REPORT: NON-MARINE MOLLUSCA

The *Atlas of the Land and Freshwater Molluscs of Britain and Ireland* will appear in April 1999, the culmination of a project launched by the Conchological Society in 1961. Some 450 recorders, mostly members of this Society, participated. It is an achievement of which we can be proud: for no other invertebrate group does so detailed a picture emerge. It is hoped that the book will be of value not just to specialists like ourselves but equally to those many people interested in our wildlife and concerned about its future.

As in the case of our provisional Atlas published in 1976, the maps were produced at the Biological Records Centre at Monks Wood, Huntingdon. I should here particularly like to thank Dr Mark Telfer, who overcame many technical problems with skill and perseverance. A grant from the Royal Society towards the cost of publication is also gratefully acknowledged.

The long-established Census scheme based on voucher specimens checked by referees will of course continue. Its principal value today is that it provides a secure basis for assessing the reliability of much larger volumes of information resulting from local surveys. The following vice-comital novelties have been verified since the last Report (*Journal of Conchology* **36**, part 4 (1999) p.59). All date from 1998, unless stated otherwise.

Cornwall East (2): *Ferrissia wautieri*, Bude Canal (21/2005); *Theba pisana*, Bude (21/2006), both Hazel Meredith.

Wilts North (7): *Boettgerilla pallens*, Leigh Delamere (31/8879), J.M.C. Hutchinson.

Hants South (11): *Pisidium moitessierianum*, R. Avon, Sopley (40/1497), I.J. Killeen, 1997. **Surrey** (17): *Limax maculatus*, Banstead (51/2757), J.M.C. Hutchinson.

Middlesex (21): *Lehmannia valentiana*, Regent's Park (51/2882), J.M.C. Hutchinson. **Norfolk East** (27): *Corbicula fluminea*, R. Chet, Heckingham (62/3899), D. Howlett. **Caernarvon** (49): *Vertigo moulinsiana*, Cors Geirch, Rhyd-y-clafdy (23/3235), B. Colville. **Anglesey** (52): *Vertigo pusilla*, Red Wharf Bay (23/5480), M.D. Sutton.

Lancaster West (60): *Abida secale*, Yealand Redmayne (34/4976), B. Colville.

Lanark (77): *Pisidium obtusale*, Springfield Reservoir (26/9052), T. Huxley.

Aberdeen North (93): *Pisidium obtusale*, Strichen Loch (38/9454), T. Huxley.

South Ebudes (102): *Arion lusitanicus*, Ardnave, Islay (16/2872; derelict croft), C. Felton. **Ross East** (106): *Vertigo genesii, Vertigo geyeri*, Braelangwell Wood SSSI, Black Isle (28/6863), M. Howe.

Cork West (H3): *Aplexa hypnorum*, Caragh Lough, Clonakilty (10/3440); *Theba pisana*, Inchydoney Island, Clonakilty (10/3938), both B. Colville.

Galway South-east (H15): *Vertigo moulinsiana*, Portumna (12/8503), Evelyn Moorkens. **Galway North-east** (H17): *Vertigo lilljeborgi*, Shankhill West Bog (12/6352), Evelyn Moorkens.

Mayo West (H27): *Vertigo geyeri*, Crossmolina (13/0522), Evelyn Moorkens.

Donegal West (H35): *Vertigo geyeri, Vertigo pusilla*, Sheskinmore (13/6895), Evelyn Moorkens.

Important discoveries continue year by year, and 1998 has been no exception. The close attention that is now being given to the fauna of ancient wetlands is rapidly increasing our knowledge of the genus *Vertigo* within the British Isles. The most notable discovery is of the rare Boreo-Alpine species *Vertigo genesii* at a further British site, in the Black Isle of Ross-shire. The habitat is a tufaceous flush with *Schoenus nigricans* and *Saxifraga aizoides*, fed by springs from calcareous Devonian sandstones. As in two of the small cluster of sites recently discovered in Perthshire the species was associated with *Vertigo geyeri* (a species also new to Ross-shire). In Ireland Dr Moorkens has found *V. geyeri* in

fens in Co. Mayo and Co. Donegal. She has also found *Vertigo lilljeborgi* in a fen in Co. Galway, and *Vertigo pusilla* (a very uncommon snail in Ireland) in a dune slack in Co. Donegal. Equally noteworthy is the discovery by Dr Colville of *Vertigo moulinsiana* in a *Cladium mariscus* fen at an isolated site in Caernarvonshire, the first time this species has been found in Wales.

Among introduced species, the Mediterranean helicid *Theba pisana* has been extending its range in recent years in S.W. Britain, and can now be recorded for Cornwall East. It has also reached southernmost Ireland. In July 1998 it was found by Dr Colville on sand dunes near Clonakilty, Co. Cork, and was also noted by Dr Martin Cawley in a similar coastal habitat some fifteen miles further east near Ballinspittle in the same vice-county (10/6043). Seaside tourism is doubtless helping to spread the snail.

Turning to freshwater species, the most noteworthy find of the year has been the discovery in a Norfolk river of a flourishing population of the bivalve *Corbicula fluminea* Müller), new to the British Isles. Growth-lines on the largest specimens suggest that the colony has been established for at least four or five years. Originally Asiatic, the species was noted in North America in the 1930s and is now widespread there. In recent years it has spread also into many European countries, including France, Germany and the Netherlands, especially along the River Rhine and its tributaries. In the USA the 'Asian clam' has proved a troublesome pest, seriously damaging aquatic habitats by sheer pressure of numbers. It is probably already too late to extirpate the Norfolk colony and we must view the possible spread of *Corbicula* in lowland England with some alarm.

Finally, an interesting rediscovery. *Myxas glutinosa* was first noted in Bala Lake (Llyn Tegid) in Merionethshire around 1850 and the species was still common there in 1952, when it was verified for the Census. (It is worth remarking that in 1936 A.E. Boycott had dismissed the Victorian records of *Myxas* from this locality as 'hardly reliable', so improbable did they seem.) Subsequent attempts to refind it failed, prompting fears that supposed changes in the habitat had caused its extinction. It is therefore gratifying to report that in September 1998 Dr Martin Willing and Dr David Holyoak noted *Myxas* living in abundance at several points around the lake, under stones in shallow water.

M.P. Kerney

MARINE RECORDER'S REPORT 1998

This reporting year saw an exciting new development in the storage and management of the Society's marine mollusc records. Stimulated by the *MarLIN* project, which is a proposal by the Marine Biological Association of the UK in association with the Joint Nature Conservation Committee, the Society has acquired a computer for the purpose of storing marine mollusc records using Michael Weideli's database programme, RECORDIT. The object of *MarLIN* is not to take control or seek ownership of databases such as ours, but rather to facilitate access through the National Biodiversity Network. In practice this means that we retain the ability to allow access to marine mollusc records tagged at varying degrees of restriction according to sensitivity to a range of users. It is hoped that as the database grows, the Conchological Society will take advantage of the service that can be provided. In particular I hope that members will use the absence of recent records from certain localities and stretches of coastline, to plan their own site visits and field recording in an attempt to fill the gaps in up-to-date information. Following acquisition of the computer, and revision and testing of the RECORDIT software, a training workshop took place in October at which a number of members received tuition in the programme. We now have a nucleus of enthusiasts who are keying in records on their home computers for transfer to the central computer. Whether these members are Sea Area Representatives, or are conducting nonmarine County-based surveys, in addition to the contribution they make to the Marine Census database, they now have the means of storing and manipulating their own records and generating distributions maps using the DMap software.

Meanwhile out in the field, the year has seen some new records for three Red Data Book species. *Tenellia adspersa* (RDB K, Insufficiently known) is a small nudibranch, distributed worldwide but for which British records are sparse. The species lives in euryhaline environments and until last year there was only one definite extant site - the Fleet, Dorset. Pam and Peter Wilson have now found the species living on the hydroid *Laomedea* sp. at St Osyth, Essex on 2 occasions (*J. Conch.* **36** (5)). The range of extant UK sites for *Paludinella littorina* (RDB 3) has been extended further west in Devon with the finding of the species in a cave at Brixham (*Conchologists ' Newsletter* no. 146) and southwards to the Channel Islands where it was found at 2 sites on Jersey during the Society field meeting (Killeen, in prep). Despite sparse and intermittent records for shells of *Truncatella subcylindrica* (RDB 3) from Cornwall spanning 1849-1976, a living specimen was only recently found in the estuary of the Percuil River last October (*J. Conch.* **36** (4)). In addition to the fact that these three species share varying RDB status, the common factor linking them is their small size and cryptozoic biology. As their ecology becomes better known and focused searching is continued, I predict that the current year will produce more records for all three species.

Further north, Shelagh Smith reports that the text of *The Marine Mollusca of West Scotland and the north coast of Ireland* is complete and that preparation of the maps is under way. This complementary publication to *The Marine Mollusca of East Scotland* has been long-awaited and will be published as soon as possible. During 1998, Shelagh's husband David Hurd found a single individual of *Calyptraea chinensis* living in Clachan Sound, Oban - this northernmost record is some considerable distance from the nearest established population for the species in Loch Ryan, Stranraer.

It is always satisfying to be able to report on new records, but I would like to acknowledge everyone who has submitted record cards and field data during the year. I would like to thank those members who have supported the recording efforts of the Society's marine field meetings and also those who are now active in building up the Society's computerised database. In this latter context my special thanks go to Mike Weideli, Colin Gillard, Christine Street and Pam Wilson.

Jan Light
March 1999

HON. PROGRAMME SECRETARY'S REPORT FOR 1998

Rupert Honnor succeeded Ian Killeen as Hon. Programme Secretary at the AGM in 1996, and held the post for two years. He arranged the programme for 1998, before standing down at the AGM. The position of Hon. Programme Secretary then became vacant.

When indoor meetings resumed on 10th October 1998, it was obvious that a Hon. Programme Secretary was urgently needed. I volunteered to co-ordinate a skeleton programme from the suggestions supplied by Council, with just ten days to do it, in order to meet the October 20th Copy Date deadline for the December 1998 *Newsletter*. Having had this "trial run" I was asked by Council at the November 7th meeting if I would agree to take on this position. I agreed, and so went on to prepare the 1999 Programme Card and further details for the March Newsletter. I have also prepared this 1998 Hon. Programme Secretary's Report.

The 1998 programme contained eighteen events. Of these, six were Lectures held at the Natural History Museum, London; three were Workshops, and nine were Field Meetings.

Lectures delivered
Molluscs of the Arabian Sea - Graham Oliver
Biogeography and Local Conservation - Presidential Address Brian Eversham
Lower Tertiary Molluscs - Adrian Rundle
After Boycott - Georges Dussart
Biodiversity Matters - Martin Willing
Review of Molluscan Survey Progress - Chaired by Ian Killeen

Workshops held
Cones at Reading Museum - June Chatfield
The Melville-Tomlin Collection at NMW Cardiff - Graham Oliver
Annual Woking Workshop, courtesy of Judith Nelson
Identifying British Vertiginidae - Adrian Rundle
Identifying the Fossil Fauna of Blockley Quarry - Phil Palmer

Field Meetings held
South Somerset Land and freshwater survey work for the Somerset Atlas: Colin Gillard.
Durham Area woodland molluscs and Zechstein reef fossils: Rosemary Hill.
Devon Marine meeting surveying for the DOMMIC (Distribution of Marine Molluscs In Channel) project: Rupert Honnor.
Hampshire Freshwater surveys in uncharted waters: Martin Willing.
Berkshire Land and freshwater surveys for the Berkshire Atlas: Mike Weideli.
Pembrokeshire Marine and non-marine excursions: Sue Davies.
Jersey Marine surveying for the DOMMIC project: Jan Light and Ian Killeen.
Surrey Surveying in old pasture woodland: June Chatfield.
Surrey Examination of the terrestrial molluscs on contrasting sites at Box Hill and Colley Hill: Keith Alexander.

I would like to thank all those who have helped to make our programmes possible during this time

Helen Weideli

REPORT OF THE HON. CONSERVATION OFFICER 1998-1999

Selected key items from the 1998-99 year are summarised below.

The Molluscan Conservation Group of Great Britain & Ireland

The work of the Conservation Officer was enhanced by the establishment of this group. Its remit is to 'maintain and enhance molluscan species and habitat biodiversity'. A more detailed description of the work and composition of the group appears in the *Conchologists' Newsletter* **147**: 113.

Biodiversity Matters

- The Conservation Officer and Journal Editor both spoke at an Environment Agency conference, 'Species management in aquatic habitats'.
- A Council Member spoke about 'rare molluscs' at the annual English Nature 'Species Recovery' seminar.
- Several Molluscan Conservation Group members are sitting upon UK Steering Groups for a number of the Biodiversity Steering Group's Priority Species. These include groups representing (1) the terrestrial species: *Vertigo geyeri, V. genesii, V. angustior, V. moulinsiana* and *Catinella arenaria* and (2) the freshwater species *Pseudanodonta complanata, Pisidium tenuilineatum, Segmentina nitida, Anisus vorticulus* and *Myxas glutinosa.*
- Several Molluscan Conservation Group members are involved in assisting/advising Alisa Watson, a recently successful PhD applicant who is embarking upon a NERC/Environment Agency Research Studentship/Fellowship aimed at determining the key habitat requirements of two Biodiversity Steering Group Priority Species.
- Molluscan information has been supplied for numerous local and regional Biodiversity Action Plans including those for West Sussex, Hampshire, Somerset and Northumbrian Water.
- Several Society members have been involved on a professional basis with survey and monitoring work on Biodiversity Steering Group Priority Species including *Anisus vorticulus, Segmentina nitida, Pisidium tenuilineatum, Vertigo moulinsiana, V. geyeri, V. genesii, Myxas glutinosa, Catinella arenaria* and *Margaritifera margaritifera.*
- A talk was given to the Society by the Conservation Officer reviewing the wide range of work occurring throughout the country involving the Biodiversity Steering Group's Priority Species.

Advice and help

Has been given to a wide range of individuals and organisations including:

- Further advice given to the R.S.P.B. re. the management of reserves in the Arun Valley.
- Help given to a number of undergraduate and postgraduate students undertaking molluscan based projects and research.
- Information given to the Environment Agency concerning ditch management on the Pevensey Levels.

British Wildlife

The production of a biannual molluscan wildlife report for this journal has continued. The appearance of this column has generated numerous molluscan enquiries from individuals and organisations.

Joint Committee for the Conservation for British Invertebrates & links with other organisations

Membership of the Committee continues providing valuable contacts with other organisations. The Conservation Officer and President have attended all meetings and chaired

one, whilst the Conservation Officer has joined the executive of this organisation. They also both attended a meeting hosted by the RSPB exploring the possibility of forming a staffed, national invertebrate co-ordinating organisation. At the time of writing a consultative 'green paper' was about to be circulated to invertebrate and other conservation organisations.

Links with other organisations
The Conservation Officer continues to attend conservation committee meetings of The Sussex Wildlife Trust and has been able to offer conservation advice regarding the management of several reserves with a high molluscan interest. He was also able to present a talk on ditch species research and management to the Sussex Biological Recorders Seminar.

Two field meetings were held to National Trust properties to assess their molluscan importance. Both meetings provided valuable data that will assist the Trust in maintaining the molluscan interest of the sites investigated. Further survey meetings on National Trust properties are planned for the 1999 season.

Members of the Molluscan Conservation Group were able to provide the Environment Agency with information and advice that has been used in the production of two Species Awareness leaflets. These are intended to aid E.A. staff throughout the country in identifying Biodiversity Steering Group Priority land and freshwater species.

Commercial exploitation of foreign shell material
Sainsbury's Homebase were again found to be marketing items containing tropical land and freshwater shells that may not have originated from the 'sustainable' sources claimed by the company. The Society is currently involved in pursuing this matter and is also producing a questionnaire which will seek to investigate the wider extent of the trade in exotic shell products at other commercial outlets.

Conservation work undertaken throughout the Society
Many other conservation activities have been undertaken throughout the year by Society members, often in a professional capacity. These are too numerous to mention individually, but range from continued work with the DOMMIC (English Channel) marine molluscan mapping project, molluscan surveys of freshwaters and wetlands throughout the country including work on the rivers Arun, areas throughout the Hampshire basin, Cornwall, the Lake District, North and South Wales, central and western Scotland.

Publicity
Members of the Society appeared on regional and radio programmes

M.J. Willing 3/1999

INSTRUCTIONS TO AUTHORS

Manuscripts should be sent to:

PAPERS   Two copies of text and illustrations should be submitted; one set of illustrations must be good quality originals. Authors should refer to *New Instructions to Authors* in this issue as a guide to format. Authors are reminded of the high cost of printing and therefore are expected to write concisely and to make maximum use of page size when designing artwork and tables.

COMMUNICATIONS   These are intended to be short notes of an original nature which do not merit the treatment of a full paper. *Communications* do not normally   contain any figures, tables or plates and should conform in style to that of recent issues of the *Journal*.

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